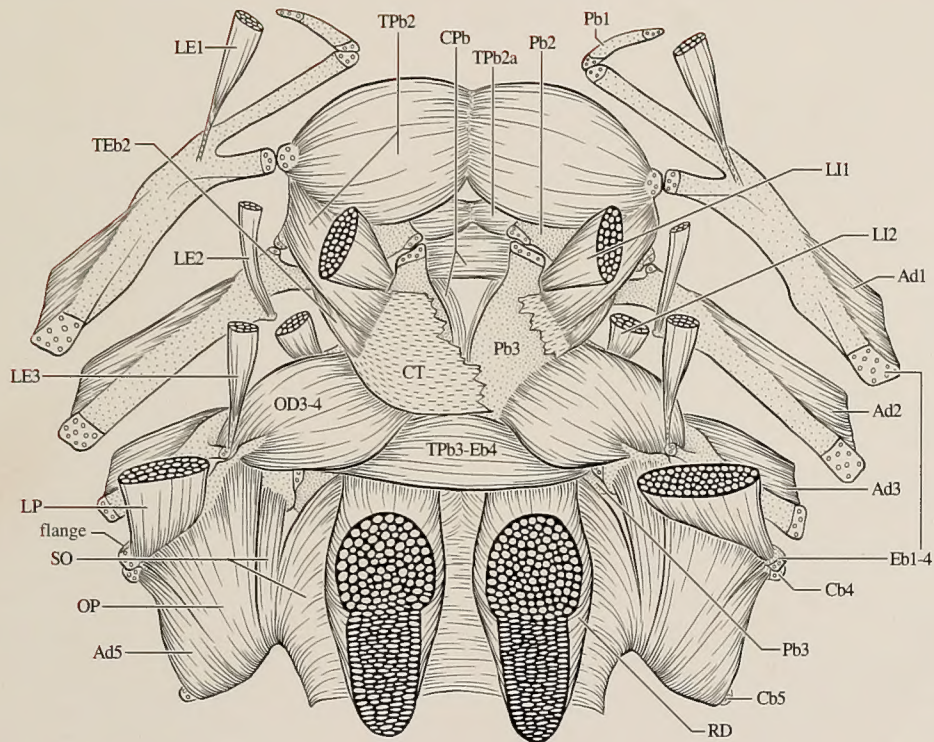


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Cover illustration: *Pholidichthys leucotaenia*, dorsal gill-arch musculature
(see Plate 169).

"This whole book is but a draught—nay, but the draft of a draft."

Herman Melville, *Moby Dick*.

STUDY OF THE DORSAL GILL-ARCH MUSCULATURE OF TELEOSTOME FISHES, WITH SPECIAL REFERENCE TO THE ACTINOPTERYGII

Victor G. Springer and G. David Johnson
Karolyn Darrow, Illustrator

Appendix: Phylogenetic Analysis of 147 Families of Acanthomorph Fishes Based Primarily on Dorsal Gill-Arch Muscles and Skeleton

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Abstract.—The dorsal gill-arch musculature (DGM), aspects of the associated skeleton, the *transversus ventralis* 4, and the semicircular ligament are described for many species in over 200 families and over 300 genera of teleostome fishes, and the DGM musculature of over 200 taxa is illustrated. A partially new system of DGM nomenclature is used. The *transversus dorsalis*, is shown to be a much more complex system than has been generally recognized. DGM data are variously analyzed and shown to be of importance for defining various currently recognized suprageneric pre-acanthomorph taxa. Among the many conclusions pertaining to acanthomorphs are: monophyly of Percopsiformes is hypothesized; Icosteidae, Menidae, and Centriscidae are probably more closely related to pre-percomorph groups than to percomorph groups; there is no basis for inclusion of Amarsipidae in the Stromateoidei; monophyly of the Polycentridae (*Polycentrus*, *Polycentropsis*, *Afronandus*, *Monocirrhus*) is corroborated based on a combination of gill-arch muscle and additional characters. A new ordinal-group name, Anabantomorpha, is erected to include the seven families with parasphenoid teeth: Nandidae, Badidae, Pristolepididae, Channidae, Anabantidae, Heleostomatidae, and Osphronemidae. Anabantoidei includes the last four of these families, which have supra-branchial organs. The superfamily name Labroidea is proposed to distinguish the unequivocally monophyletic group of families, Labridae, Odacidae, Scaridae, from other families included in the suborder Labroidei. The first synapomorphy for the gobioid family Odontobutidae is hypothesized based on the position of the *levator internus* 2 relative to the *obliquus dorsalis*. Certain gill-arch skeletal characters previously unrecognized or inadequately evaluated are reported and discussed (e.g., epibranchial-ceratobranchial accessory cartilages; relationship of epibranchials 5 and 4; epibranchial 4 flange; esophageal raphe).

A separately authored appendix provides a cladistic analysis of 168 taxa in 147 acanthomorph families based almost exclusively on DGM and gill-arch skeletal characters. Among the many results implied by the study are: monophyly of Percopsiformes is corroborated. Smegmamorpha Johnson and Patterson (1993) are polyphyletic, and the name is rejected for nomenclatural purposes. Its constituents comprise two or three not closely related clades: Mugilomorpha + Atherinomorpha (= Percosoces Cope, 1875), Gasterosteomorpha, and, possibly, Centrisciformes (a pre-percomorph group, comprising only Centriscidae). Gasterosteomorpha includes a monophyletic Hypoptychidae (*Hypoptychus* + *Aulichthys*), Ellassomatidae, Aulorhynchidae, monophyletic Synbranchiiformes (Synbranchidae + Mastacembelidae), and Gasterosteidae, thus corroborating various hypotheses of Johnson and Patterson (1993) and Johnson and Springer (1997). Labroids are monophyletic only with inclusion of Pholidichthyidae, but the group remains supported only by pharyngognath characters. Blennioidei are monophyletic and their intra-relationships resolved. Their closest relatives are, stepwise: Gobiesocidae, Draconetidae (+ Callionymidae, which were not included in the analysis), Dactylopteridae. A new ordinal-group name, Benthomorpha, is proposed for this clade. Caproidae are polyphyletic; relationships of its two genera appear to be with tetraodontiforms on the one hand, and acanthuroids, on the other. As such, Johnson and Patterson's (1993) hypothesis that caproid relationships are among percomorphs is corroborated. Sphyrænidae and Polynemidae form a monophyletic group (first proposed by Regan, 1912).

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This study was initiated about 1996 as the primary effort of the first author (VGS), who had long been interested in determining the interrelationships of the acanthomorph family Pholidichthyidae. Springer and Freyhof (1976) last discussed the problematic interrelationships of the then monospecific family (Springer and Larson, 1996, described a second *Pholidichthys* species). Subsequently, Stiassny and Jensen (1987), expanding on the work of Kaufman and Liem (1982), hypothesized the composition and interrelationships of an acanthomorph suborder Labroidei. Stiassny and Jensen based their hypothesis on a relatively broad selection of acanthomorph fishes and almost exclusively on a limited number of gill-arch characters. Referring only to Springer and Freyhof's (1976) study, they noted similarities of the gill-arch skeleton of *Pholidichthys* to that of the labroids.

Johnson (1993:9–10) discussed errors of oversight and commission in Stiassny and Jensen's (1987) study and noted, critically, that, other than characters associated with pharyngognathy, there was none that corroborated monophyly of the labroids. VGS re-examined *Pholidichthys* in light of Stiassny and Jensen's and Johnson's studies, and noted problems with both, although he agreed with Johnson's general criticism. As a result, VGS, with the assistance of GDJ, undertook to survey a wide variety of acanthomorph fishes to determine the distribution of the states of the muscle characters used by Stiassny and Jensen. VGS expanded the study to include a broad spectrum of non-acanthomorph fishes because of problems in determining muscle homologies among the acanthomorphs.

Darrow joined the project as full-time illustrator in the fall of 1997 and remained on the project until mid-2000, after which she continued on contract and then as volunteer until late 2003, when all the gill-arch muscle illustrations were completed.

VGS contracted with Tom Orrell to run PAUP program analyses of a limited number of acanthomorph taxa beginning in 2002, but in 2003 involved him in the preparation of the major cladistic analysis forming our co-authored Appendix to the present study.

After essentially completing the actinopterygian pre-acanthomorph portion of the study, including an

analysis of the data, and much of the descriptive portion of the acanthomorphs, joint efforts with GDJ ceased in early 2002 at the sole instigation of VGS.

VGS is responsible for selecting most of the taxa used in the study, preparing a large majority of the dissections, all the descriptions, supervision of preparation of all the illustrations, the partially new system of nomenclature used to designate the muscles, the interpretation and results of the non-acanthomorph portion of the study, most of the acanthomorph interrelationships, discussions that are not outgrowths of the cladistic analyses, all of the choices of taxa, characters, and character codes for the cladistic analyses, and preparation of all preliminary and final drafts of the entire manuscript. *I, VGS, therefore, accept full responsibility for all errors, factual or otherwise, and eccentricities that this study embodies.* On the other hand, I gladly share with my co-authors responsibility for any favorable aspects of the study. I especially want to thank them for their input: GDJ for his early encouragement and important suggestions for taxa to include, ready and comprehensive knowledge of the existing classifications of many groups of fishes and their defining characters, and his often constructive challenges, his critical reading of an early complete draft of the pre-acanthomorph section of the actinopterygian portion of the study, early drafts of a large number of the acanthomorph descriptions and discussions, commenting on a near final draft of the pre-Appendix portion of the manuscript, and very importantly, for bringing Karie Darrow to my attention; Karie Darrow for her dedication to the project, even after monetary compensation ceased, and the unstinting use of her great illustrative talents, as well as for the numerous occasions on which she caught my descriptive mistakes; and to Tom Orrell for his insightful and knowledgeable handling of the PAUP program used in the phylogenetic analysis, important suggestions for the preparation and interpretation of the output, and patience under stress of my importunities.

In the pre-Appendix portion of the text that follows, the editorial "we" and "our" are used to accord with authorship, but their use is not intended to imply agreement by the second author.

Introduction

The present study has two main purposes. First, to provide an annotated, descriptive atlas of the dorsal gill-arch muscles of the extant fishes (coelacanth, lungfishes, actinopterygians) included in the Superclass Teleostomi (= Grade Teleostomi, in part, of Nelson, 1994:65) or Osteichthyes (= branch 8 of Gill and Mooi, 2002:fig. 2.2) with special reference to the Actinopterygii. Second, to determine how the character states exhibited by these muscles accord with existing morphologically based phylogenetic classifications of the fishes, and to a much lesser extent, molecular-based classifications.

Because our study initially involved two ventral gill-arch structures (notably, the semicircular ligament and the *transversus ventralis* 4), we also surveyed them. We variously include treatment of other ventral gill-arch muscles and muscles that span both the dorsal and ventral gill-arch elements. On the other hand, as a result of the way the study developed, we did not survey the *protractor pectoralis*, which is often closely associated with the dorsal gill-arches. We regret this omission, but the muscle was destroyed during preparation of many of the gill-arches before we realized its potential importance (for an extensive survey of this muscle see Greenwood and Lauder 1981).

In our attempts to provide accurate illustrations of the muscles and their attachments, we also attempted to apply the same attention to the dorsal gill-arch skeletal elements. We frequently illustrate and discuss skeletal structures that were previously unreported or erroneously described. On the other hand, we do not address all the skeletal characters that have been used in previous classifications, only those that are obvious in the illustrations, have direct bearing on the position of muscle attachments, or that by chance came to our attention (e.g., whether infra-pharyngobranchial 2 is present or absent, and if present bears teeth or is edentate).

In a study as broad as ours, keeping up with relevant literature was a problem. Although, we attempted to do this, we recognize the possibility that references will have been missed. Another problem is that of references that became available after our discussion and analyses were in an advanced state and to adjust for them would have required continual revision and delay of the study. As far as we are aware, we have included and adjusted for the literature published through the end of 2002, and much of the literature of 2003.

Methods

Dissections were made and studied primarily using a Zeiss Operation Technoscope. Drawings were made using a Wild M-3 stereoscopic microscope with at-

tached camera lucida. As required, details were checked using a high resolution Leitz stereoscopic dissecting microscope.

In general, gill arches were removed from specimens using the following procedure. First, the hyoid arches including the branchiostegals were either separated from the membranes connecting them to the opercular series and the interhyal linking them to the hyomandibula and retained attached to the gill-arches, or, usually, the gill arches were released from the hyoid arches by separating the hypohyals from the basibranchials. The basihyal was then freed by making a semicircular incision around the floor of the mouth. Next, the gill filaments were stripped off while trying to assure that the external and posterior levators were not removed with them (*levator externus* 1 and *levator posterior*, require the most care to avoid damage or removal). Tissue enclosing the gill-arch musculature laterally was then removed. Particular care was necessary at this point as the *levator externus* 4, *levator posterior*, and *protractor pectoralis* in some forms (e.g., clupeomorphs, lampridiforms) may be closely applied or imbedded in the tissue and would be damaged or removed with the tissue. A cut was then made across the pharyngeal roof just anterior to the gill arches and pharyngobranchial 1, if present, and the latter was released from its attachment to the skull. Muscles, ligaments, bones, nerves, and blood vessels attaching the gill arches to the skull were carefully scraped or cut free. A cut was then made through the pre-pectoral area to free the ventral attachment of the gill arches to the body (cut passes through ventral aorta and, depending on taxon, may slice through the urohyal). From this cut, a posterodorsally arching cut was made on each side of the specimen in the tissue containing the *pharyngocleithrales* and attaching the gill arches to the surface of the cleithrum. The *sphincter esophagi* was then severed and the *retractor dorsales* severed from their attachments to the vertebrae. Any attached tissues (viscera, nerves, etc.) were cut and the gill arches released. The variety of taxa dissected frequently required considerable ad hoc modifications to this general procedure.

After removal, the gill arches were partially cleaned by picking away the most obvious blood vessels, nerves, viscera, and extraneous fatty and connective tissues. The gill arches were then stained. Early in the study we used a KOH-alizarin red-s solution to stain bone and an acetic acid-ethyl alcohol solution of alcian blue to stain cartilage (Dingerkus and Uhler 1977). We found, however, that the KOH-alizarin solution was destructive of the muscles and we substituted a non-destructive ETOH-alizarin solution (Springer and Johnson 2000) for it. Regardless of which alizarin solution was used, the muscles usually acquired a pink color or, in the case of alcian, a

blue-green color, enabling one to distinguish them more easily from one another or surrounding tissues. After staining, the muscles were further cleaned of extraneous tissues and described.

Descriptions and illustrations were often done in stages. In the first stage, as much information as possible was recorded without disturbing the muscles other than to truncate the levators, if they obscured the other muscles. The muscles were then drawn. In the next and subsequent stages, muscles were bisected or removed in order to expose hidden muscles or muscle attachments, and at each stage, the drawing was modified, usually unilaterally, to show additional information. Levator muscles and the *retractor dorsalis* are truncated, without mention in most of the illustrations.

Some muscle attachments were inferred without dissection by referring to cleared and stained preparations. In so far as they were not removed during cleaning, ligaments and miscellaneous connective tissues are included in the illustrations and mentioned in the descriptive accounts, but the absence of such structures from the illustrations or descriptions does not necessarily imply that they are actually absent.

We strove for clarity in the illustrations, at the same time attempting to portray the muscles as closely as possible to their actual appearance—bilateral asymmetry and anomalies were included. Photographs would have been more accurate, perhaps, but much less clear. The plates, with a few exceptions noted in the plate legends, are based on single specimens. The specimen illustrated may not be typical of the taxon in every detail illustrated. For this reason, if the reader notes a difference between a character as coded in the PAUP data matrix (Appendix, Table 12) and the representation of that character in the illustration, the description of the taxon should be read for explanation. All such conflicts, however, may not be explained, e.g., proportional or presence-absence characters that are distorted resulting from parallax or are obscured in the view illustrated.

Finally, during the course of determining obscured muscles and skeletal elements, the muscles of many of the specimens were of necessity greatly damaged or removed and the specimens will be of limited or no use to future investigators. This is particularly true of specimens that were prepared early in the study using a KOH-alizarin solution to stain the bones, as the solution badly macerates the muscles, and its residue continues to do so over time.

Material

Institutional abbreviations denoting specimens are those proposed by Leviton et al. (1985) and Leviton and Gibbs (1988).

Relevant study material is reported at the begin-

ning of each descriptive account. If an illustration is indicated, the first indicated specimen is usually the one illustrated. Occasionally, additional material examined for only one or a few characters is cited in the text. A list of material (see Acanthomorpha section), specifically for acanthomorphs, not otherwise mentioned in the text, was examined for osteological information, and served as the source for information in Table 8. In general, small specimens in the range of 50–150 mm SL were selected for dissection. Depending on the taxon, these may have been adults or juveniles (some taxa rarely attain a length of even 50 mm as adults; specimens longer than 150 mm were used for taxa with proportionally small heads, e.g., eel-like forms). For many taxa, only one specimen was available for study, but even for taxa where more specimens were available, only one specimen may have been studied if the dissection was successful (i.e., little or no damage). We recognize this deficiency, but in a survey of the magnitude of the present one, we had to limit the depth of our examinations: any taxon could have been the basis for an independent study, and we dissected about 500 specimens comprising 208 families and about 400 species.

Muscles are highly variable in their expression, sometimes varying bilaterally in the same individual, between individuals of the same species, or ontogenetically. Where our material and examinations permitted, and we considered the variation important, we discuss variation.

Muscles and Skeletal Elements

The muscles mentioned in the text and on the illustrations are listed with their definitions and the abbreviations we use to represent them in the section “Abbreviations and Definitions for Anatomical Structures.” The skeletal elements are similarly included, but only some are defined. A discussion of epibranchial 5 (Eb5) is given below because the interpretation of the presence or absence of this element is important in deciding the attachment of adductor 5, and we use the opportunity to note new phylogenetic inferences based on the relationship of Eb5 to Eb4, ceratobranchial 4 (Cb4), and Cb5 (see section below, “Epibranchials 5 and 4”).

Muscle names.—There is a wealth of names available for many gill-arch muscles, but relatively few are standardized. Winterbottom (1974b) valiantly and most recently attempted a synonymy of teleost fish musculature. We utilize many of the names he recognized as senior synonyms and that are commonly employed in the literature (e.g., *levator externus*, or external levator). However, we also use a few names he treated as synonyms, and for many muscles we devise our own names. For these last muscles, our

intent is to have the name indicate the attachments of the muscle, e.g., *musculus laminalis dentalis 5-ceratobranchialis 4* (M. UP5-Cb4), a muscle originating on upper pharyngeal tooth plate 5 and inserting on ceratobranchial 4. Such names may be unwieldy, but they are descriptive, and one rarely needs to refer to them other than by their abbreviations. There is no law of priority with regard to muscle names, and we find that despite Winterbottom's attempt to standardize muscle names, complete standardization in the literature has not occurred, e.g., names of ceratodontid muscles have not been standardized. There is the additional problem, which we have not solved, of assuring homology of usage. Our nomenclature is based variably on morphological topology and/or homology. If the reader is in doubt of our usage from the context of our application or discussion, it is probably safest to assume topology.

Muscle types.—Aside from functional anatomical types (e.g., contractors, extensors), we recognize two general positional types of dorsal gill-arch muscles, those that are bilaterally paired, i.e., present on each side, and those that are transverse, extending from one side to the other. An interpretive problem develops when the middle portion of a transverse muscle is lost, as often occurs in acanthomorphs (e.g., *transversus pharyngobranchialis 2* of Pomacentridae, Plate 160; *transversus epibranchialis 2* of Embiotocidae, Plate 162.1); we have no evidence for the transverse fusion of a bilaterally paired muscle).

Origins and insertions.—Levators originate on the cranium, or in the case of the levator posterior, may originate from the body musculature. Bilaterally paired muscles attaching pharyngobranchial elements to epibranchials and/or ceratobranchials are considered to originate on the pharyngobranchial elements. Retractores dorsales are considered traditionally to originate on the vertebral column and insert on pharyngeal elements. Muscles attaching an epibranchial to another epibranchial (*recti dorsales* = RecD) on the same side of the gill arches are considered (traditionally) to originate on the more posterior epibranchial: RecD4 originates on epibranchial 4 and inserts on epibranchial 3.

Anatomical orientation.—Anterior and posterior are defined by the dorsal mid-longitudinal axis of the fish that runs between the pharyngobranchials. Medial, or proximal, and distal, or lateral, are, in effect, positions relative to the pharyngobranchials. Anterior and posterior refer to the positions relative to the head and tail of a fish, but the medial angle of articulation of epibranchials, and of the ceratobranchials with the epibranchials, often imposes an almost longitudinal orientation on them—thus, the proximal and distal ends of the epibranchials deceptively appear to be the anterior and posterior ends. The de-

scriptions are based on the anatomical position, not the deceptive appearances.

The major axis of a pharyngeal element may be oriented almost perpendicularly, in which case its anterior end may be described as dorsal and its dorsal surface described as posterior.

Transverse muscles.—Interpretation of the individual muscles comprising the *transversus dorsalis* frequently involved subjectivity because of the nature or degree of continuity between the various components. Some components were unambiguously definable, but others were not (e.g., what degree of separation of the components of *transversus pharyngobranchialis 3-epibranchialis 4* (TPb3-Eb4) should exist before recognizing the components as separate muscles, TPb3 and TEb4: only complete discontinuity of the components; continuity, but by only a few muscle fibers, etc.?). For some taxa, where more than one specimen was dissected, the components might be continuous in one specimen and discontinuous in another. The interpretations, therefore, contain a degree of subjectivity, which the illustrations reflect.

Acanthomorph accessory cartilages.—Rosen (1984:3, 25, fig. 25a) first noted the presence of an accessory cartilage (AC) at the joint of an epibranchial and ceratobranchial in the gill arches of an acanthomorph (the fourth arch of *Acanthurus*), in which he indicated that it was of unknown significance. Rosen and Patterson (1990:9, fig. 42a) next called attention to an acanthomorph AC (in *Lobotes*, also in the fourth arch) and again indicated that it was of unknown significance, neglecting to mention Rosen's earlier finding. We know of no other reports of accessory cartilages at the Eb-Cb joints of acanthomorphs, which is the only group in which they occur. Among acanthomorphs, Eb-Cb joint accessory cartilages are predominantly restricted to perciforms (Table 8). Although ACs may occur in any gill arch, they are most commonly associated with the fourth arch. In acanthomorphs having AC4, Ad5 usually attaches to it.

AC4 superficially resembles Eb5, which, as first noted by Baldwin and Johnson (1996), is restricted to pre-acanthomorphs (here further restricted to pre-Ctenosquamata, see Table 6). Based on examination of larvae of a few taxa (Osmeridae, *Osmerus*, 17 mm SL; Characidae, *Corynopoma*, >4 mm SL; Chlorophthalmidae, *Chlorophthalmus*, 12–13 mm SL), Eb5 is autogenous early in ontogeny (but may fuse ontogenetically with Eb4 and/or Cb4). In contrast, the acanthomorph AC4 is always associated with the distal (usually posterodistal) end of Cb4, and appears to bud off Cb4 relatively late in ontogeny.

In larval *Morone* (Moronidae) as large as 14 mm SL (all gill-arch elements with substantial ossification and vertebral column fully differentiated and ossi-

fied), AC4 is absent and there is no evidence of a cartilaginous projection from Cb4 from which AC4 might form. In a 28 mm SL specimen of *Morone*, there is a projection extending from the cartilaginous tip of Cb4, which, we presume is the precursor of the autogenous AC4 present in the much larger specimens of *Morone* (100 mm SL) used for the muscle descriptions. Among four cleared and stained specimens of *Ambassis* sp., USNM 218805, AC4 on both sides of two specimens, 30.7–35.4 mm SL, appear to be in the process of budding off; one specimen, 39.0, has autogenous AC4s on both sides, and one specimen, 45.6 mm SL, has an autogenous AC4 on one side, and a bud on the other. In a specimen of *Ambassis buruensis*, USNM 305331, 55 mm SL, a well-developed process extends posteriorly from the distal end of Cb4 with no evidence that budding off might occur.

Although we did not investigate them, AC1–3 and AC5 (the last known only in *Lates*, Latidae) probably also develop as buds off the distal ends of Cb1–3 and Cb5, with which they are very closely associated (CT surrounding the cartilaginous distal ends of the Cbs envelops the associated AC).

There is a problem in polarizing the character state of AC4, but based on its appearance in *Velifer*, we arbitrarily treat its presence as an acanthomorph synapomorphy.

Epibranchials 5 and 4.—The occurrence and interpretation of Eb5 has received considerable attention (Nelson 1967d; Greenwood and Rosen 1971; Rosen 1974; Fink and Fink 1996; Johnson and Patterson 1996, 1997). It has not been established, however, that the element, which is always cartilaginous, is an epibranchial (Nelson 1969a:520, reported Eb5 was ossified on one side of one specimen of a gymnotid).

Eb5, which is usually constrained as articulating with the distal end of Eb4 (e.g., Nelson 1969a:520), is reported to be lacking in all ctenosquamates (Baldwin and Johnson 1996:372).

Eb5 varies from being completely autogenous to partially fused with the distal end of Eb4, to putatively, completely fused with the distal end of Eb4, or infrequently, as we believe, with the distal end of Cb4 (only *Albula*). We find that in most groups with an autogenous Eb5, it is more closely associated with the distal end of Cb4 than it is with Eb4, and it appears to be fused with Cb4 in *Albula* based on comparison with Eb5 and its association with Cb4 in *Pterothrissus*, also Albulidae).

Except for *Osmerus* (Osmeridae), it is problematic if Eb5 is always present in taxa in which the element is interpreted as partially or completely fused to Eb4. The possible alternatives are that it has been completely lost secondarily after fusion, or lost independently before fusion. Johnson and Patterson (1996:

275) observed that Eb5 is autogenous in *O. mordax* larvae, but becomes fused to Eb4 in later stages. Fink and Fink (1996:231) reported an autogenous Eb5 in a *Gonorynchus* larva, 18.5 mm SL, which is not present at later stages, but Johnson and Patterson (1997:597), who examined Fink and Fink's specimens, were unable to find this cartilage. We also examined Fink and Fink's (1996:231) specimens (partially erroneously cited; see Johnson and Patterson 1997:597, for correct citation) and confirm Johnson and Patterson's findings.

In the plesiomorphic clupeomorph, *Denticeps*, the autogenous Eb5 attaches ventrally to the dorsodistal surface of Cb4 and anteroventrally to the ventrodistal end of the rod-like Eb4. In clupeoids with an autogenous Eb5, however, the element attaches ventrally to the dorsodistal end of Cb4 and articulates closely dorsally and ventrally, but not in between, with the vertically expanded mostly bony distal end of Eb4 (e.g., *Dussumieria*, Plate 29:B). Eb5 thus forms the cartilaginous distal border of a foramen through which the posteriormost efferent artery passes (Nelson 1969a:520); the proximal border of the foramen is mostly bony. Based on this landmark foramen, Nelson considered that Eb5 is present in clupeomorphs in which there is no joint line dorsally between it and the dorsodistal end of Eb4, but there is one at the ventrodistal end (foramen complete), or the ventral portion of the foramen is open (foramen incomplete). Nelson did not specifically indicate the fusion of Eb5 with Eb4 in those clupeomorph taxa in which the foramen is complete or the foramen is completely surrounded by cartilage with no joint line dorsally or ventrally. One can reasonably assume (as did Rosen 1974), however, that based on the configuration of the distal end of Eb4, that Eb5 is present and that it has fused dorsally and ventrally with Eb4.

There also appears to be inferential support for fusion of Eb5 and Eb4 in certain salmoniforms. In salmonids, Eb5 is either autogenous (e.g., *Oncorhynchus*, Plate 36) or, apparently, fused dorsally with Eb4 (e.g., *Prosopium*, foramen open ventrally; Rosen, 1974:fig. 9e). Johnson and Patterson (1997:596–597) appear to accept Eb5 as present in the ostariophysan *Gonorynchus* based on the ventrally open foramen in the elongate posterior cartilaginous extension of Eb4.

Circumstantial evidence based on the attachments of adductor 5 (Ad5) supports the probable fusion of Eb5 with Eb4 in pre-acanthomorphs: Ad5, which always attaches to Cb5 at one end, almost always attaches to an autogenous Eb5 at the other end, or to the distal end of Eb4 when Eb5 is putatively fused with Eb4 (Table 6).

Probably extrapolating from the clupeomorph conditions in which Eb5 is fused dorsally to Eb4 and the foramen is open ventrally, Nelson (1967d:75, fig. 1d;

also our Plate 7) considered that Eb5 might be present in the plesiomorphic osteoglossomorph *Hiodon*. In other osteoglossomorphs, the state of the foramen is variable and, with the exception of *Pantodon*, mimics the states of the clupeoids. Only *Pantodon*, among the osteoglossomorphs, has an autogenous Eb5 (Plate 13B), but its articulations (one end with Cb4 and the other with an accessory cartilage attaching to Cb5) are different from those that might give rise to the putatively fused conditions seen in the other osteoglossomorphs.

Excluding *Albula*, we code three character states for Eb5 (Table 6): absent (0), autogenous (1), and putatively partially or completely fused with Eb4 (2). State 2 is interpreted based on the appearance of the distal end of Eb4 (presence of a complete or incomplete foramen). If the Eb5 character states are applied to the pre-acanthomorph cladogram, it must be concluded parsimoniously that state 2 evolved independently in the Osteoglossomorpha and Clupeoidei; hence, there is no evidence for the existence of an independent or fused Eb5 at the base of the Osteoglossomorpha (the autogenous Eb5, and its articulations, in *Pantodon* is an autapomorphy). Eb5 autogenous first appears as a basal synapomorphy in the Elopoccephala.

Perhaps, ontogenetic studies of the osteoglossomorphs will reveal, as in *Osmerus*, that an autogenous Eb5 is present and becomes fused with Eb4 during development. If such is the case, however, the fusion of Eb5 to Eb4 would still have been achieved independently by the Clupeocephala.

There is another possible solution to the problem: the existing cladogram is incorrect. If Osteoglossomorpha is replaced by Elopomorpha and placed as the sister group of the Clupeomorpha, an autogenous Eb5 becomes a synapomorphy of the newly composed Teleostei, and a fused Eb4-Eb5 becomes a synapomorphy of the Clupeomorpha + Osteoglossomorpha. The reason for suggesting these changes is that Arratia (1999), based on a limited number of recent taxa, but citing studies by other authors who used additional characters, proposed that Elopiformes are the sister group of all other Teleostei and that the Osteoglossomorpha are close to the Clupeomorpha. The distribution of suprapharyngobranchial 1 (SPb1) also makes more sense parsimoniously if the Elopomorpha exchange places with the Osteoglossomorpha in the cladogram (see discussion of LI1 in pre-acanthomorph Results section).

This extended discussion bears on character states for the attachment of Ad5. To differentiate states in which Ad5 attaches to an autogenous Eb5 from those in which it attaches to a putatively (partially or completely) fused Eb5 with Eb4 or Eb5 with Cb4, we indicate the latter two skeletal conditions as "Eb4*" or "Cb4*." We indicate these abbreviations, where

applicable, in the discussions and on the illustrations of the Elopoccephala, but not the Osteoglossomorpha.

Abbreviations and Definitions for Anatomical Structures

Note: the following definitions occasionally contain important caveats on the interpretation of certain muscles, e.g., ER, the esophageal raphe.

*—following a pre-acanthomorph Eb4 or Cb4 indicates putative fusion of Eb5 with Eb4 or Cb4. See section "Epibranchials 5 and 4" for discussion.

AB—autogenous bone; tiny bone attached to tip of Eb4 levator process and dorsal end of Eb5; only in Cyprinidae.

AC—accessory cartilage; mostly restricted to acanthomorphs. Among pre-acanthomorphs having ACs (*Polypterus*, *Atractosteus*, *Pantodon*, *Diplomystes*, *Galaxias*), the ACs may occur in a variety of locations and may be normal or adventitious in the taxon in which they occur. Among acanthomorphs, ACs are common, but occur predominantly at the joint between the distal ends of an Eb-Cb pair, hence AC1, AC2, etc., with AC4 the most common in occurrence. Except for the rarely occurring AC5, acanthomorph ACs occurring at positions other than at an Eb-Cb joint are not numbered. See section "Acanthomorph accessory cartilages" for discussion.

Ad—adductor, adductores. Ad1, Ad2, etc., adductor of 1st arch, 2nd arch, etc; plural, Ads, Ad1s, etc.; muscle attaching Eb to Cb of a single arch, except Ad5, which attaches Cb5 variously to one or more of the following: Cb4, AC4, Eb4, or Eb5. Ad4 dorsal attachment is on dorsoposterior or ventral surface of Eb4, often beginning anterior to OP on Eb4 and usually extending laterally further than OP. When present, one or more of first three Ads may be completely obscured by, or fused with, an overlying gill-filament muscle (GFM, q.v.) of same arch. In general, Ads are better developed than GFMs. We occasionally had difficulty distinguishing Ads from GFMs in acanthomorphs, and subjectivity in deciding may have resulted in some erroneous decisions.

Among, pre-acanthomorphs, Ads1–3 occur only in Polyodontidae, Notacanthidae, Cyprinidae, and possibly Anguillidae. They are variably present among acanthomorphs, most commonly among percomorphs. It is unlikely that Ad1–3 of pre-acanthomorphs and acanthomorphs are homologues. It is unlikely, furthermore, that the acanthomorph Ads1–3, which are absent in basal acanthomorphs, are serial homologues of Ad4 and Ad5 in acanthomorphs, which occur early in pre-acanthomorph phylogeny.

The identification of Ad5 in various non-perci-

form acanthomorphs in which ER is also present can be problematic. In some cases, it appears that Ad5 is absent, in others Ad5 ends dorsally at a raphe with the ventral end of OP, and in others that Ad5 is present as the lateral portion of what otherwise appears to be OP. In pre-acanthomorphs, apparent fusion of Ad5 medially with OP ventrolaterally is common. Additional study of ER, Ad5, and OP is warranted. See also OP below and remarks following Ad5 in description of *Arapaima* (Arapaimidae).

Ad4'—adductor 4 primus, attaches to the anterodistal surfaces of Eb4 and Cb4 (additional to Ad4); only in Notacanthidae.

Bb—basibranchial, Bb3, Bb4, etc.; unpaired ventral gill-arch skeletal element.

Cb—ceratobranchial; plural, Cbs; also Cb1, Cb1s, etc.; ventral gill-arch skeletal element.

CPb—*circumpharyngobranchialis*; a sub-epithelial muscle first described, but not named, by Anker (1978:261) for a cichlid muscle, and apparently not reported subsequently. CPb is present in various perciform fishes and is often very well developed. It appears to originate from the SO longitudinal muscle layer, extending anteriorly, and surrounding or only bordering, and attaching variously to Pb2, Pb3, and UP4. In some perciforms (e.g., cichlids, pomacentrids) TPb2a, may represent a disjunct portion of CPb.

CT—connective tissue.

Eb—epibranchial; plural, Ebs; also, Eb1, Eb1s, Eb2, etc.; dorsal gill-arch skeletal element.

Eb4* indicates putative fusion of Eb5 with Eb4; only in pre-acanthomorphs.

Epibranchial flange—a dorsolateral or anterolateral extension of the dorsodistal bony edge of an epibranchial such that it partly or completely “shields” the cartilaginous distal end. Present only in some percomorphs and usually restricted to Eb4, although flanges may be present on other Ebs. The flanges are much reduced in size in many taxa (and difficult to show on our illustrations). A well-developed Eb4 flange is present, e.g., in all members of the Labroidei, Opistognathidae, Pseudochromidae, Grammatidae; variably developed in Plesiopidae (well developed in *Assessor* and *Paraplesiops*; weakly developed in *Trachinops* and *Belo-nepterygion*; absent in *Acanthoplesiops* and *Noto-graptus*); well developed in all atherinomorphs except very weakly developed in belonids and absent in scomberesocids. Also very weakly developed in the mugilid, *Agonostomus*. In labroids, the cartilaginous distal end of Eb4 has been lost and the cartilaginous end of Cb4 attaches by a tendon to the ventral surface of the flange.

EO—epibranchial organ; plural, EOs; in pre-acanthomorphs usually formed, at least in part, by mod-

erate to extraordinary expansion of the cartilaginous distal end of Eb4; in acanthomorphs (only stromateoids), EO involves an out pouching of the esophagus and distal end of Eb4 is not involved. Certain anabantoid families (e.g., Channidae, Anabantidae) have a suprabranchial organ which involves modification of the first epibranchial.

ER—esophageal raphe; a fine line of connective tissue or myoseptum usually dividing OP transversely at about mid-level or demarcating the ventral end of OP and separating it from Ad5 and/or SO. Very common in pre-acanthomorphs, but frequently difficult to decide the constitution of the muscle fibers ventral to ER: SO, OP, or Ad5. Relatively uncommon in acanthomorphs, but when present usually appears to separate OP ventrally from Ad5, resulting in OP attaching ventrally to Cb4 rather than Cb5 (its usual ventral attachment in acanthomorphs), and Ad5 attaching to Cb4 well medial to distal end of bone, rather than to the distal end.

GC—gongyloid cartilage, first named by Di Dario (2002) and first described by him in print, but first noted by Nelson (1966a:157) in his Ph.D. dissertation; present only in engrauloids, pristigasteroids, and *Chanos* (Chanidae). See discussions in Additional remarks sections under *Cetengraulis* and *Chanos*.

GFM; GFM1, 2, 3—gill filament muscle. Here considered to be essentially the same as Winterbottom's (1974b:260 and fig. 26c) *interbranchiales abductores*: “extrinsic [gill] filament muscles . . . connecting the bases of the oral filaments to the gill arch (cerato- or epibranchial [we would modify this to cerato- and/or epibranchial]) . . . may [also] become intimately associated with the gill rakers . . .” They are often inconspicuous, fine, and stringy and are frequently destroyed when stripping gill filaments from the gill-arches. Those of the second and third arches in acanthomorphs may extend dorsoanteriorly and attach to the posterior edge of the preceding arch or they may continue dorsomedially on the dorsal surfaces of Eb2 and Eb3, that of the second arch sometimes meeting the lateral end of TEb2. We report them only in some acanthomorphs, and only when they are conspicuous or fused with an adductor (Ad). In some taxa, they are questionably distinct from Ads (q.v.); decision on assignment as GFM or Ad is somewhat arbitrary. Additional study of the acanthomorph Ads and GFMs is desirable.

Winterbottom (1974b:259–260 and fig. 26) also recognized *interbranchiales adductores*, muscles attaching to the gill filaments of both hemibranchs of a single gill arch. We do not report on these muscles.

Hb—hypobranchial; Hb1, etc.; plural, Hbs; ventral gill-arch skeletal element.

IAB—interarcual bone; a putatively ossified IAC, only in Synbranchidae and Carapidae.

IAC—interarcual cartilage; usually an autogenous rod-like cartilage joining Eb1 uncinat process to Pb2; found only among acanthomorphs.

IAC2—interarcual cartilage 2; autogenous cartilage joining Eb2 and Pb2; only in Menidae.

Interbranchiales abductores, adductores—see GFM.

LCb—*levator ceratobranchialis* (i.e., LCb2, LCb4, LCb5) muscle originating on skull and inserting on a Cb; only in pre-acanthomorph Cyprinidae and acanthomorph Adrianichthyidae. See also remarks following LCb5 in muscle description of Cyprinidae for comment on homology. Not to be confused with LE5 of Dipnoi, which inserts on Cb5.

LCb5A—*levator ceratobranchialis 5 accessorius*; muscle originating in supratemporal fossa of skull near origin of LCb5, wrapping medially first, then anteriorly around LCb5 and inserting in CT pad attached to anterolateral surface of Cb5; only in Cyprinidae. This muscle appears to be the same as Holstvoogd's (1965:216, and fig. 12b) M. trochlearis, which Winterbottom (1974:253) synonymized with LP. It is also the same as Winterbottom's LP internus (internus and externus portions not labeled), as indicated in his fig. 22 (*Cyprinus*). Muscle re-named by us at suggestion of R. Winterbottom, who correctly noted (in litt.) that trochelar most often refers to cranial nerve IV, which supplies the superior oblique muscle of the eye, hence, inappropriately applied to a gill arch levator.

lat—lateral.

LE—*levator externus* or external levator; muscle originating on cranium and inserting on an Eb: LE1, LE2, etc.; plural LEs, LE1s, etc. With rare exception (Carapidae), LEs originate on the skull, typically in a cluster or continuous line, usually together with LIs; however, LE4 may be displaced posteriorly in some taxa, especially those with EOs (see also LP). LE3 always inserts on or close to the Eb3 uncinat process in elopoccephalans (ignoring those taxa in which the uncinat process is absent). According to Vanderwolle et al. (1998), all carapid levators originate on the medial surface of the hyomandibula.

LE1', LE2', etc.—*levator externus 1 primus*, etc.; the second of two LE1s, etc., arbitrarily designated, presumably the result of the division of an LE.

Levator process (on Eb4)—a cartilaginously tipped process, lateral or posterior to the uncinat process (q.v.) on which LE4 and/or LP usually inserts. Presence or absence of the process may be ontogenetically associated: process isolated from distal cartilaginous end of Eb, or, in acanthomorphs, cartilage lost during ontogeny by osseous exclusion. In the absence of a cartilage tip, the process is

arbitrarily considered absent.

Johnson and Patterson (1996:272–275) discuss the confusion and phylogeny of uncinat and levator processes on Eb4 and note that an Eb4 uncinat process “characterizes acanthomorphs,” and that “Loss of a separate levator process appears to be a synapomorphy of Acanthopterygii, although it may occasionally occur secondarily within Percomorpha . . .” The presence of an Eb4 levator process in percomorphs is more common than Johnson and Patterson implied. It is frequently present in generally considered plesiomorphic percomorphs (e.g., Acropomatidae, Percichthyidae, Moronidae, Scorpaenidae, Epigonidae, Apogonidae, Serranidae, Lutjanidae, Priacanthidae, Lateolabridae etc.) as well as in some specialized members (e.g., Opistognathidae, Trachinidae).

LI—*levator internus* or internal levator; muscle originating on cranium and inserting, variously, on Pb2, Pb3, Pb4, UP4, or UP5 (LI1, LUP5, etc.; plural, LIs, LI1s, etc.); LI1 inserts on Pb2 (and/or Pb3 in some acanthomorphs; especially Blennioidei, which lack Pb2); LI2 normally inserts on Pb3; LI3, absent in ctenosquamates, variously inserts on Pb3, Pb4, UP4, UP5; LI4, only in Diplomystidae, inserts on UP4. Some confusion may arise when comparing our LIs with those mentioned in the literature, as many authors number the LI based on the Pb to which it attaches; hence our LI1 is often referred to as LI2 in the literature, our LI2 as LI3, and our LI3 as LI4.

LI1a, LI1p—*levator internus 1 anterioris, levator internus 1 posterioris*; LI1 represented by two longitudinally separated muscles, both inserting on Pb2; only in Myctophidae.

LI1'—*levator internus 1 primus*; the posterior division of LI1 inserting on Pb3 anteriorly, often closely juxtaposed to LI1 insertion on Pb2; frequently present in, but not limited to, Gobioidae.

LI3 (part)—a separate, probably anomalous, basal portion of LI3; only in *Heterotis* (Osteoglossomorpha).

LI3'—*levator internus 3 primus*; second of two LI3s inserting on Pb4; only in *Searsia*, (Platytrichidae).
lig—ligament.

LP—*levator posterior* (or *levator posterioris*); mostly restricted to acanthomorphs, but present in some clupeoids and ostariophysans. Muscle originating variously on skull or body musculature and usually inserting on Eb4 together with LE4. In some taxa, fused with LE4 or coalesced in a muscular and connective tissue sheet with LE4 and/or PP, which attaches along edges of gill arches 4 and 5, and the individual muscles are not clearly separable. When LP is clearly distinguished, its origin is posterior or posteromedial to LE4 origin and usually well removed from it. In taxa with a single levator

muscle on Eb4 (including, however, LE4') that originates with other LEs and/or LIs, there is no problem identifying the muscle as LE4 (and LE4') because LP never clusters with the other LEs. In pre-acanthomorph taxa that have the origin of the single levator on Eb4 well posterior to those of the other levators, one might be tempted to designate the muscle LP, but examination of the muscles in related forms invariably indicates that only LE4 is present (i.e., it joins LE cluster). Additionally, LE4 generally inclines anteriorly, whereas LP frequently inclines medially or anteromedially. Only three acanthomorph taxa appear to have lost LE4 and retained LP: *Pholidichthys* (Pholidichthyidae), *Spinachia* (Gasterosteidae), and, possibly, Echeeniidae.

med—medial.

mid—middle.

M.—*musculus*; muscle.

M. Eb1-Cb1—*M. epibranchialis 1-ceratobranchialis 1*; muscle joining dorsomedial end of Eb1 with dorsoanterodistal end of Cb1 (only in Callionymidae).

M. Eb1-IAC—*M. epibranchialis 1-cartilago interarcualis*; muscle originating on Eb1 and attaching to IAC (only in Adrianichthyidae).

M. Eb4-F—*M. epibranchialis 4 faucis*; muscle originating on Eb4 and meshing with SO in throat (Latin, *fauces*) region (only in Blenniidae).

M. Intrb—*M. intrabranchialis* (pl. *intrabranchiales*); M. Intrb1, Intrb 2 etc; muscle present in the CT (variously termed a diaphragm or septum) between the hemibranchs of a single branchial arch, overlain by the gill filaments, which must be scraped away to expose it. Known only for Chondrichthyes, in which they have been termed *interbranchiales* (Marion, 1905:905 & figs. 7, 8, 12; Daniel, 1934:105 & fig. 108) or *constrictor branchiales* (Edgeworth, 1935:129), and Dipnoi, in which they have also been termed *interbranchiales* (Fürbringer, 1904:488) or *constrictor branchiales* (Edgeworth, 1935:129; Fox, 1965:490). Here renamed to avoid confusion with the “*interbranchiales*” (which include *interbranchiales adductores* and *abductores*), originally named by Winterbottom (1974b:259 & fig. 26) for small teleostean muscles attaching to the gill filaments (see also GFM). Edgeworth (1935:129) erroneously reported M. Intrbs in acipenserids (see Additional remarks section under *Acipenser ruthenus*).

M. Pb2-Eb1—*M. pharyngobranchialis 2-epibranchialis 1*; muscle originating on Pb2 and inserting on Eb1; only in mormyrids and some anguilliforms.

M. Pb2-Eb2—*M. pharyngobranchialis 2-epibranchialis 2*; muscle originating on Pb2 and inserting on Eb2. According to Winterbottom's (1974b:253)

definition of obliqui dorsales, any muscle originating on a Pb and inserting on an Eb could be termed an OD, but to do so might cause confusion. Our M. Pb2-Eb2 has been designated OD2 by Endo (2002:101) for gadiforms, in which he considered its presence a specialization. In pre-acanthomorphs, OD2 is present only in the osteoglossomorphs (*Hiodon* and *Heterotis*), where it originates on Pb3.

In most acanthomorphs, the muscles we treat as obliqui dorsales originate entirely or primarily on Pb3 and insert on Eb3 and/or Eb4. To distinguish the acanthomorph OD2 (in *Brotula*, which also has M. Pb2-Eb2), we elected to denominate the “OD” originating on Pb2 as a new muscle: M. Pb2-Eb2; likewise, we designate other “ODs” as M. Pbs-Ebs to avoid confusion. See also OD.

M. Pb3-Cb5—*M. pharyngobranchialis 3-ceratobranchialis 5*; muscle originating on Pb3 and inserting on Cb5 (only in Sparidae and Centrarchidae).

M. Pb3-Eb1—*M. pharyngobranchialis 3-epibranchialis 1*; muscle originating on Pb3 and inserting on Eb1 (only in Callionymidae).

M. Pb3-Eb2—*M. pharyngobranchialis 3-epibranchialis 2*; muscle originating on Pb3 and inserting on Eb2 (only in Pomatomidae).

M. Pb3-Eb3-Eb4—*M. pharyngobranchialis 3-epibranchialis 3-epibranchialis 4*; muscle originating on Pb3 and inserting on Eb3 and Eb4 (only in gobiid *Gnatholepis*).

M. Pb3-Eb3—*M. pharyngobranchialis 3-epibranchialis 3*; muscle originating on Pb3 and inserting on Eb3 (among pre-acanthomorphs, only in *Novumbra*, Umbridae; among acanthomorphs, at least in some gobioids).

M. Pb3-Eb3-Eb2—*M. pharyngobranchialis 3-epibranchialis 3-epibranchialis 2*; short muscle originating on Pb3 and inserting on Eb3 and Eb2 (only in Gymnarchidae).

M. Pb3-Eb4-Eb2-Cb3—*M. pharyngobranchialis 3-epibranchialis 4-epibranchialis 2-ceratobranchialis 3*; muscle originating on Pb3 and inserting on Eb4, Eb2, and Cb3 (only in *Callionymus*).

M. Pb3p—*M. pharyngobranchialis 3-posterior*; short cone-like muscle attaching anteriorly to Pb3 and inserting, apparently without attaching, into a concavity at the anterior end of the first vertebra. Function problematic; found only in Hemiramphidae and Exocoetidae.

M. Pb3-Pb4-Eb2—*M. pharyngobranchialis 3-pharyngobranchialis 4-epibranchialis 2*—muscle originating on Pb3 and Pb4 and inserting on Eb2; only in the osteoglossomorph Gymnarchidae.

M. Pb3-UP4—*M. pharyngobranchialis 3-laminalis dentalis 4*; muscle attaching to Pb3 and UP4; only in Embiotocidae.

M. Pb4-Eb2—*M. pharyngobranchialis 4-epibranch-*

- chialis* 2; muscle originating on Pb4 and inserting on Eb2; only in notopteroids.
- M. SO-Pb2—*M. sphinctoris esophagi-pharyngobranchialis* 2; muscle originating on each side as an anterior extension of the transverse layer of the sphincter oesophagi, becoming discrete anteriorly as it extends along medial side of Pbs and inserts on Pb2 and, variously, Eb4; noted in leiognathids, but probably more widely distributed.
- M. SO-Pb3—*M. sphinctoris esophagi-pharyngobranchialis* 3; muscle originating on each side as an anterior extension of the dorsal SO longitudinal muscle layer, becoming discrete anteriorly and inserting on Pb3. More common than noted in the descriptions or on the plates as it was identified late in the study (e.g., *Ditropichthys*, Cetomimidae, Plate 74).
- M. SO-Pb4—*M. sphinctoris esophagi-pharyngobranchialis* 4; dorsolateral extension of SO that attaches to Pb4, only in *Psenopsis*, Centrolophidae.
- M. SPb2-Eb2—*M. suprapharyngobranchialis 2-epibranchialis* 2; interrupted portion of LE2 originating ventrolaterally on SPb2 and inserting on Eb2; only in Acipenseridae.
- M. SPb2L—*M. suprapharyngobranchialis 2 lateral*; interrupted portion of LE2 originating on skull and inserting on SPb2 dorsolaterally; only in Acipenseridae.
- M. SPb2-LE1—*M. suprapharyngobranchialis 2-lelevator externus* 1; probably a component of LE2 originating from CT on medial surface of LE1 and inserting anteriorly on mid-medial surface of SPb2; only in Acipenseridae.
- M. SPb2Ma—*M. suprapharyngobranchialis 2 medialis anterior*; interrupted portion of LE2 originating on skull and inserting on SPb2 anteromedially; only in Acipenseridae.
- M. SPb2Mp—*M. suprapharyngobranchialis 2 medialis posterior*; interrupted portion of LE2 originating on skull and inserting on SPb2 posteromedially; only in Acipenseridae.
- M. TEb2-Pb2—*M. transversus epibranchialis-pharyngobranchialis* 2. A part of TD arising from ventral surface of TEb2 and inserting on Pb2; not homologous with TPb2, which arises dorsal or anterior to TEb2; only in Cepolidae.
- M. UP4-Eb2—*M. laminalis dentalis 4-epibranchialis* 2; muscle originating on UP4 and inserting on Eb2; only in *Albula*.
- M. UP4-Eb4—*M. laminalis dentalis 4-epibranchialis* 4; muscle originating on UP4 and inserting on Eb4; only in Congridae.
- M. UP4-Eb5-Cb4—*M. laminalis dentalis 4-epibranchialis 5-ceratobranchialis* 4 (not illustrated); muscle originating on UP4 and inserting on Eb5-Cb4 joint; only in Megalopidae.
- M. UP5-Cb4—*M. laminalis dentalis 5-ceratobranchialis* 4; muscle originating on UP5 and inserting on Cb4; very similar to M. UP5-Cb4-Eb5; only in Albulidae and Gonostomatidae.
- M. UP5-Cb4-Eb5—*M. laminalis dentalis 5-ceratobranchialis 4-epibranchialis* 5; muscle originating on UP5 and inserting at inner angle of joint formed by Cb4 and Eb5; only in characoids, but very similar to M. UP5-Cb4.
- MPb1—mediopharyngobranchial; cartilage articulating posteriorly with anterior or medial end of Eb1; may comprise single, medial element; present only in Chanidae, Gonorhynchidae, and some Clupeoidei.
- ObV3—*obliquus ventralis* 3 (not illustrated); ventral gill-arch muscle attaching to Hb3 and Cb3; may also insert on SCL.
- OD—(plural, ODs) *obliquus dorsalis (obliqui dorsales)*. We follow convention in describing these muscles as originating on Pbs and inserting on Ebs. Gareth Nelson (commenting on a draft of the MS) noted that, functionally, it is more accurate to reverse the origin-insertion designations.
- ODs usually originate on Pb3, but origin may include Pb1 (only *Diplomystes*, Diplomystidae) and Pb4 (only pre-acanthomorphs) and Pb2 (only acanthomorphs). Designation derives from Eb on which muscle inserts. See M. Pb2-Eb2 for discussion of why this muscle is not considered to be an OD.
- OD2—origin on Pb3; only in osteoglossomorphs.
- OD3—insertion on Eb3 includes uncinat process, if present.
- OD3'—origin on Pb3 with, ventral to, or lateral to OD3 or OD3-4, becomes ventral to them posteriorly, and attaches on Eb3 dorsally ventral or medial to uncinat process; except for *Oncorhynchus*, present only in acanthomorphs.
- OD3-4—a complete or almost complete fusion of OD3 and OD4, essentially restricted to acanthomorphs, in which origin is usually restricted to Pb3 and insertions usually on Eb3 and Eb4 bony surfaces supporting cartilaginous tips of uncinat processes.
- OD4—in pre-acanthomorphs originates on Pb3, Pb3 and Pb4, or Pb4; in acanthomorphs originates almost exclusively on Pb3; insertion on Eb4 includes bony surface supporting cartilage tip of uncinat process, if present.
- OD4v—small ventral branch of OD4; only in *Heteropriacanthus* (Priacanthidae).
- OD4'—originates on Pb4 in all pre-acanthomorphs except *Megalops* and *Brycon*, in which it originates on Pb3. Among acanthomorphs, OD4' is only present in percopsiforms, in which it originates dorsal to OD4 or OD3-4 on Pb3, extends posteriorly dorsal to them and inserts on the Eb4 levator process.

OP—*obliquus posterioris*; highly variable muscle, sometimes in as many as four parts, attaching dorsally to the posterior surface of Eb4, usually medial to dorsal attachment of Ad4, but often almost completely overlapping Ad4 posteriorly. In most pre-acanthomorphs, OP is usually interrupted transversely at mid-length by ER, and in most of the few acanthomorphs that have it, ER usually separates the ventral end of OP from Ad5 (see discussion in Ad). OP medially is frequently inseparable from SO or ventrolaterally from Ad5. In some pre-acanthomorph (e.g., *Amia*) and most acanthomorph taxa, OP is continuous, uninterrupted by ER, and attaches ventrally to Cb5 near attachment of Ad5, although OP ventromedial edge may join a restricted raphe with Ad5 posterodistally.

Aerts (1982) reported that OP in cichlids comprises three separate sections: medial, central (here termed middle), and lateral, and that LE4 fuses with the middle OP section to form a continuous muscle extending from the origin of LE4 to the attachment of the OP middle section to Cb5. This combined muscle has been called a “sling” by Lauder and Liem (1983:171) and Stiassny and Jensen (1987:284), and it also occurs in (but is not limited to) labrids (broad sense), embiotocids, and, perhaps (our opinion) pomacentrids, and may include participation by LP. Most acanthomorphs only give evidence of having one OP section, most probably the middle section; we may have missed the divisions early in our work and further study is desirable.

OP'—*obliquus posterioris primus*; slender muscle (possibly anomalous) originating on Eb4 levator process and joining ER with OP; only in Albulidae.

PP—*protractor pectoralis*; muscle of pectoral girdle, occasionally illustrated and/or discussed, but only when included in a CT sheet also containing, and usually not clearly distinguishable from, LE4 and/or LP. Greenwood and Lauder (1981) provide an extensive survey of this muscle in fishes.

Pb—pharyngobranchial (commonly truncated spelling for “infrapharyngobranchial”; used for convenience); Pb1, Pb2, etc.; dorsal gill-arch skeletal element.

PC—*pharyngoclavicularis*, -es (or *pharyngocleithralis*, -es), ventral gill-arch muscle, usually two on each side, but only one present on each side in eels and pre-halecostomes, but that of pre-halecostomes may be divided. See also PCE, PCI below.

PCa, PCp—*pharyngoclavicularis anterioris*, -posterioris; divisions of the single PC of the pre-halecostome *Polypterus*.

PCE, PCI—*pharyngoclavicularis externus*, -internus (of Winterbottom, 1974b:267); ventral gill-arch

muscles attaching Cb5 to the cleithrum; both present on each side in most halecostome actinopterygians; one or both frequently illustrated in our plates but usually not discussed (absence in illustrations not intended to imply actual absence). PCI is illustrated or described in all acanthomorph taxa in which the muscle attachment includes the distal end of Cb5 and/or joins a raphe with OP ventrally.

PrO—*protractor pharyngeus*, anteriorly inclined levator-like muscle originating on ventral cranial surface, extending posteriorly, and inserting on dorsal non-musculous esophageal connective tissue; present only in *Neoceratodus* (Dipnoi).

RCb5E—*retractor ceratobranchialis 5 externus*; muscle originating on ventral basioccipital process and inserting dorsolaterally on Cb5; only in Cyprinidae.

RCb5I—*retractor ceratobranchialis 5 internus*; muscle originating as CT along dorsolateral surface of vertical SO fold abutting basioccipital process and inserting by long tendon on CT pad attaching to Cb5; only in Cyprinidae.

RCb5T—*retractor ceratobranchialis 5 transversus*; muscle originating medially from CT and SO, and inserting on dorsolateral margin of Cb5; only in Cyprinidae. Appears to be the same as retractor pharyngeus superioris of Winterbottom, 1974b: 258; fig. 22b). Only in Cyprinidae.

RD—*retractor dorsalis*; muscle usually originating on anterior vertebrae and inserting variously on one or more of Pb3, Pb4, UP4, UP5, and Eb4. Origin and insertion usually not described by us. RDs may insert anteriorly or posteriorly on Pbs, and the difference is probably important. RDs may be unpaired, branch only at beginning of insertion, comprise a bilateral pair (one RD on each side), a bilateral pair and smaller unpaired median member (RD'), or vertical pair of muscles on each side. RD varies from being incorporated almost entirely within the SO (ventral to the circular or transverse muscle layer) to being entirely external to SO (see also SOD).

RD' indicates either the unpaired median muscle between the individual RDs of a bilateral pair or the dorsal muscle when RD consists of vertical pair of muscles on each side (see RD).

RecCb—*rectus ceratobranchialis*; short muscle connecting distal ends of two successive Cbs; only in Callionymidae.

RecCom—*rectus communis*, a ventral gill-arch muscle infrequently and only incidentally appearing in the illustrations; not discussed in descriptions.

RecD—*rectus dorsalis* (plural *recti dorsales*); muscle typically joining epibranchial on one side with epibranchial immediately anterior; RecD2, RecD3, RecD4, number derives from posterior epibranchial, i.e., RecD2 originates on Eb2 and inserts on

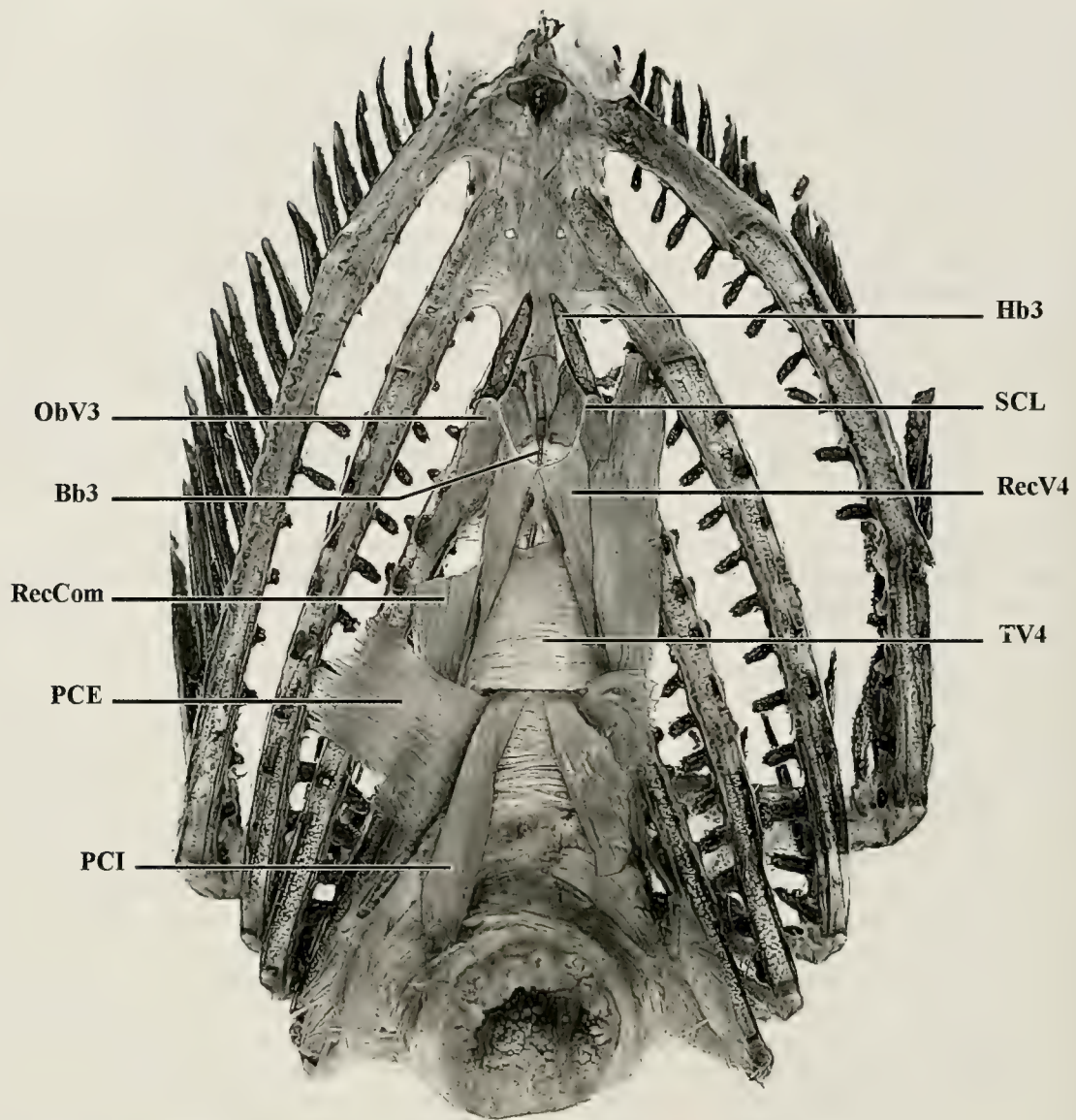


Fig. 1. Ventral view of gill-arches of *Pempheris schomburgkii*, USNM 318588 to show semicircular ligament (SCL). Both RecComs greatly truncated; left-side PCE almost completely removed; basihyal removed. Ventrally elongate cartilaginous tip of posterior end of Bb3 joins SCL mid-posteriorly. Photograph extensively retouched.

Eb1; RecD1, however, originates on Eb1 and probably inserts on skull or peters out in skin that roofs mouth; RecD5 (only *Callionymus*) origin includes Cb5, insertion includes various skeletal elements anteriorly. We have applied RecD to a variety of problematic muscles found in clearly unrelated taxa (e.g., Menidae, Callionymidae, Cyprinidae, Anguillidae). See also discussion following RecDs in *Callionymus*.

RecV4—*rectus ventralis 4* (Fig. 1); ventral gill-arch muscle attaching Cb4 to Hb3 and/or SCL.

SCL—semicircular ligament (Fig. 1); anteriorly open U-shaped ligament attaching anteriorly to the ventromedial ends of Cb3 and Cb4 and, often, mid-posteriorly to ventral surface of cartilaginous posterior end of Bb3, which, in acanthomorphs, is of-

ten elongate and ventrally recurved. The ventral aorta divides into left and right branches, which pass anteriorly on either side of the Bb3 attachment. ObV3 and RecV4 usually attach to SCL. The attachment of SCL to Bb3 is often obscured in ventral view, and the connection is easily broken during dissection or in trying to determine if it is attached to Bb3. Several character states for the Bb3 attachment to SCL were apparent in our dissections, but because of intermediates, we analyzed SCL only for presence or absence. When we are certain of our observation, we report when SCL is attached to Bb3. In the descriptions, where SCL is merely described as present, we are uncertain as to whether it was free or attached to Bb3. Stiassny (1992:269–271) discussed and illustrated

SCL. Her statement that SCL is an “acanthomorph innovation” is incorrect as SCL is present in several pre-acanthomorphs (Table 1; SCL of *Novumbra* is especially similar to that of acanthomorphs).

SL—standard length; all specimen lengths are SL, unless indicated otherwise.

Sling—see OP.

SO—sphincter esophagi; as generally recognized in the literature.

SOD—sphincter esophagi division; a narrow to broad band of SO transverse, or circular, muscle separated dorsally from the remainder of the transverse layer and passing dorsal to RDs. We imprecisely restrict SOD to the condition in which RD extends noticeably anteriorly external to SOD before entering the transverse muscle layer (thus excluding the Aulopiformes and Ateleopodiformes as having SOD). SOD cannot be present if RD is absent, but SOD is not always present when RD is present. Although apparent in some of the acanthomorph illustrations, we may have failed to record the presence of a fine, often inconspicuous mid-ventral branch of SOD that separates the left and right RDs.

SPb—*Suprpharyngobranchial*; dorsal gill-arch skeletal element of endochondral origin articulating with the cranium and, normally, with Eb1 (SPb1) or Eb2 (SPb2); present only in *Latimeria* and some actinopterygians (i.e., Chondrostei, Ginglymodi, Amiidae, Elopiformes, Albuliformes, and Platyroctidae).

TD—*transversus dorsalis*; transverse muscles attaching the gill-arch elements on one side with those on the other; not labeled as such on plates. Comprises TDA and TDP and their components. TDA and TDP muscles may be continuous and on the same level, or, most commonly in acanthomorphs TDA is somewhat dorsal to the level of TDP. TDA may be broadly or narrowly continuous with TDP or completely separate. TDP muscles may be continuous posteriorly with SO or SOD. Same names for component muscles of TDP or TDA reported in different taxa do not necessarily imply homology; likewise, different names in different taxa may obscure homology.

TDA—*transversus dorsalis anterior*; transverse muscles attaching to the anterior skeletal elements: Pb2, Eb1, Eb2 (e.g., TEb2; Pb3 attachments in acanthomorphs generally not reported in muscle names for TDA muscles); not labeled as such on plates. In acanthomorphs, the medial portion of a TDA muscle may be lost or replaced by tendinous tissue or a thick CT pad, resulting in a pair of muscles, each of which may attach secondarily to an additional skeletal element, e.g., interrupted TEb2, might attach to Pb3 as well as to Eb2.

TDP—*transversus dorsalis posterior*; transverse

muscles, attaching to the posterior skeletal elements: Eb3, Eb4, Pb4, UP4 and/or to Pb3 in the area joining these elements (e.g., TPb3-Eb3); not labeled as such on plates.

TD plexus—slender muscle branches joined to a median CT sheet dorsal to TD; branches attach to Eb1, Eb2, and Eb3; only in *Acanthurus* (Acanthuridae).

TEb1—*transversus epibranchialis 1*; essentially restricted to Labridae, Odacidae, Scaridae.

TEb1-Eb2—*transversus epibranchialis 1-epibranchialis 2*; only in *Pantodon* (Osteoglossoidei).

TEb2—*transversus epibranchialis 2*. Muscle may appear to comprise two more-or-less fused segments, giving impression of twisting (see especially Gobiidae) as they pass between levators (usually LI1 and LI2) to insert on Eb2.

Borden (1999) differentiated a muscle he termed TD2 from another he termed OD2 in *Naso* (Acanthuridae) on the basis that TD lacks a mid-line raphe and OD2 has one. Although usually present, the presence or absence of a raphe and its extent when present are highly variable, and we recognize a single muscle, TEb2, for Borden's TD2 and OD2. See also M. TEb2-Pb2.

TEb2a—*transversus epibranchialis 2 anterioris*; in pre-acanthomorphs only in *Maurolicus* (Stomiiformes), variously in acanthomorphs (e.g., *Pseudapocryptes*, Gobiidae; labroids).

TEb2p—*transversus epibranchialis 2 posterioris*; in pre-acanthomorphs only in *Maurolicus* (Stomiiformes), variously in acanthomorphs (e.g., *Pseudapocryptes*, Gobiidae; *Dicrolene*, Ophidiidae).

TEb2v—*transversus epibranchialis 2 ventralis*; only in *Diplophos* (Stomiiformes).

TEb2-Eb1—*transversus epibranchialis 2-epibranchialis 1*; only in *Beryx* (Berycidae), not to be confused with TEb1-Eb2.

TEb3—*transversus epibranchialis 3*; present only in acanthomorphs. Except for the pre-acanthomorph engraulid genus *Coilia*, attachment of TD to Eb3 alone or together with another skeletal element, is restricted to Acanthomorphs, and is a synapomorphy of the group.

TEb3-Eb4—*transversus epibranchialis 3-epibranchialis 4*.

TEb4—*transversus epibranchialis 4*. May be discrete or continuous anteriorly and/or posteriorly with other muscles.

TPb1-2-3-Eb1-2—*transversus pharyngobranchialis 1,2,3-epibranchialis 1,2*; only in *Diplomystes* (Diplomystidae).

TPb2—*transversus pharyngobranchialis 2*. In pre-acanthomorphs and primitive acanthomorphs, this is frequently a band-like muscle anterior to TEb2, if latter is present, and usually attaches to both Pb2s. In acanthomorphs, beginning with paracan-

thops and zeoids, TPb2 lies partly or entirely dorsal to TEb2 and fuses partly or entirely ventrally with TEb2, and, except for its loss or the loss of TEb2, rarely if ever has any other topographical position. TPb2 may also be pad-like or consist of a bi-lateral muscle pair usually joined by CT; may comprise a medially open semicircular ribbon of muscle on each side, which may join only TEb2 antero- and posteromedially, or may attach anteriorly only to IAC, Pb2, or Pb3. Occasionally, it may be present only unilaterally and vestigially as a semicircular ribbon. Recognition of TPb2, when not attached to Pb2 (e.g., *Rhamphocottus*, *Morene*), is based on the configuration of the muscle, which appears the same in other taxa in which it attaches to Pb2. For these reasons, we ignored the presence of an attachment to Pb2 as the defining factor in the identification of TPb2.

TPb2 deserves more study than we were able to devote to it, and our designations of the various states of the muscle as TPb2 or some variety of it, possibly obfuscates its various homologies.

In most acanthomorphs, our TPb2 is the same muscle Anker (1978) designated as the "m. cranio-pharyngobranchialis 2," which designation has been followed by most recent authors, and especially Stiassny and Jensen (1987). The muscle that the latter authors treat as the transversus pharyngobranchialis 2, we nominate as TPb2a, as it appears to have a different history from our TPb2.

TPb2'—*transversus pharyngobranchialis 2 primus*; a separate dorsoanterior portion of TPb2 (e.g., *Hoplostethus*, Trachichthyidae) or separate muscle between TPb2 and TPb3 (e.g., *Tylosurus*, Belonidae).

TPb2-Pb2a—*transversus pharyngobranchialis 2-pharyngobranchialis 2 anterioris*. Putative fusion of TPb2 and TPb2a (only in *Labroides*, Labridae, but see TPb2-Pb2a-Pb3).

TPb2a—*transversus pharyngobranchialis anterioris* (see also CPb and discussion of TPb2 above). Most prominently present in labroids, atherinomorphs, *Pholidichthys*.

TPb2d—*transversus pharyngobranchialis dorsalis*. Name applied to muscle of variable structure dorsal to and continuous with TPb2 or TPb2v in a few acanthomorphs (e.g., *Aphredoderus*, Aphredoderidae; *Agonostomus*, Mugilidae). In *Agonostomus*, it is flat, pad-like and attaches to IAC and is, perhaps, also represented by anterior portion of TPb2 in moronids and mullids.

TPb2p—*transversus pharyngobranchialis posterioris*; a posterior separation of TPb2.

TPb2v—*transversus pharyngobranchialis ventralis*; muscle joining ventral surfaces of Pb2s (e.g., Hemiramphidae). The designation might be applied to TPb2a of *Pholidichthys*, but it appears that Pb2 has rotated so that its anterior surface lies ventral; the

muscle is more similar to TPb2a of atherinomorphs than it is to TPb2v of atherinomorphs.

TPb2-Pb2a-Pb3—*transversus pharyngobranchialis 2-pharyngobranchialis 2 anterioris-pharyngobranchialis 3*. Compound muscle comprising a fusion of TPb2, TPb2a, and TPb3 (only in *Symphodus*, Labridae).

TPb2-Pb3a—*transversus pharyngobranchialis 2-pharyngobranchialis 3 anterioris*; present only in some aulopiforms.

TPb2-Pb3-Eb4—*transversus pharyngobranchialis 2-pharyngobranchialis 3-epibranchialis 4*; only in *Gymnarchus* (Osteoglossomorpha).

TPb2-Pb3-Pb4-Eb4—*transversus pharyngobranchialis 2-pharyngobranchialis 3-epibranchialis 4*; only in *Lovettia* (Galaxiidae).

TPb3—*transversus pharyngobranchialis 3*; commonly present in a large variety of fishes.

TPb3-Eb3—*transversus pharyngobranchialis 3-epibranchialis 3*; only and commonly present in acanthomorphs (see also TEb3).

TPb3-Eb3-Eb4—*transversus pharyngobranchialis 3-epibranchialis 3-epibranchialis 4*; only in acanthomorphs (see also TEb3).

TPb3-Eb4—*transversus pharyngobranchialis 3-epibranchialis 4*.

TPb3-Eb4-UP4-UP5—*transversus pharyngobranchialis 3-epibranchialis 4-laminalis dentalis 4-laminalis dentalis 5*; only in *Anguilla* (Anguillidae).

TPb3a—*transversus pharyngobranchialis 3 anterioris*; only in pre-acanthomorphs.

TPb3a-Eb2—*transversus pharyngobranchialis 3 anterioris-epibranchialis 2*; only in a few pre-acanthomorphs.

TPb3p—*transversus pharyngobranchialis 3 posterioris*, only in pre-acanthomorphs.

TPb3p-Pb4—*transversus pharyngobranchialis 3 posterioris-pharyngobranchialis 4*; only in a few pre-acanthomorphs.

TPb3-Pb4-Eb3—*transversus pharyngobranchialis 3-pharyngobranchialis 4-epibranchialis 3*; only in acanthomorphs.

TPb3p-Pb4-Eb3-Eb4—*transversus pharyngobranchialis 3 posterioris-pharyngobranchialis 4-epibranchialis 3-epibranchialis 4*; only in veliferids and some girellids.

TPb3'—*transversus pharyngobranchialis 3 primus*; posteriormost of three TPb3s (after TPb3a, TPb3p); only in *Aulopus* (Aulopidae).

TPb3-Pb4—*transversus pharyngobranchialis 3-pharyngobranchialis 4*; in various pre-acanthomorphs, but only in *Bovichtus* (Bovichtidae) among the acanthomorphs.

TPb3-Pb4-Eb4—*transversus pharyngobranchialis 3-pharyngobranchialis 4-epibranchialis 4*; present

- only in a few acanthomorphs, *Psenopsis* (Centrolophidae), *Tetracentrum* (Ambassidae).
- TPb3p-Pb4-Eb4—*transversus pharyngobranchialis 3-posterioris-pharyngobranchialis 4-epibranchialis 4*; only in pre-acanthomorphs, e.g., *Searsia* (Platyroctidae).
- TPb3-UP3-UP4—*transversus pharyngobranchialis 3-laminalis dentalis 3-laminalis dentalis 4*; only in the eel *Synphobranchus* (Synphobranchidae).
- TPb3-UP4—*transversus pharyngobranchialis 3-laminalis dentalis 4*; present *Xenocephalus* (Uranoscopidae) and some gobioids.
- TPb3p-UP4—present only in *Albula* (Albulidae).
- TPb3-UP4-Eb4—*transversus pharyngobranchialis 3-laminalis dentalis 4-epibranchialis 4*; present only in one species of *Channa* (Channidae).
- TPb4—*transversus pharyngobranchialis 4*; present in a variety of pre-acanthomorphs, but only in *Pseudaphritis* (Pseudaphritidae) among the acanthomorphs.
- TPb4a—*transversus pharyngobranchialis 4 anterioris*; an almost completely separate anterior section of TPb4.
- TPb4-Eb3—*transversus pharyngobranchialis 4-epibranchialis 3*; only in *Coilia* (Clupeoidea) and *Nemipterus* (Nemipteridae).
- TPb4-Eb4—*transversus pharyngobranchialis 4-epibranchialis 4*; present only in pre-acanthomorphs.
- TUP4—*transversus laminalis pharyngobranchialis 4*; only in gobioids *Pseudapocryptes* and *Ptereleotris*.
- TUP4a—*transversus laminalis dentalis 4 anterioris*; only in *Diplomystes* (Diplomystidae).
- TUP4p—*transversus laminalis dentalis 4 posterioris*; only in *Diplomystes* (Diplomystidae).
- TUP5—*transversus laminalis dentalis 5*; muscle connecting UP5s; only in Stomiiformes.
- TL—total length.
- TV4—*transversus ventralis 4* (Fig. 1); ventral gill-arch muscle connecting Cb4 on one side to Cb4 on the other; dorsally interrupted in some acanthomorphs (e.g., labroids) and attaching also to Cb5.
- TV5—*transversus ventralis 5*; ventral gill-arch muscle connecting Cb5 on one side to Cb5 on the other; occasionally illustrated, but not described.
- Uncinate process (pertaining to Ebs1–4; occasionally refers also to Pb2, which may have a distinct process that articulates directly or indirectly with Eb1 or Pb3)—defined for our purposes as a cartilage-tipped process. Hence, if the cartilage tip is absent the process is considered absent; however, with regard to Eb1, Eb3, and Eb4, if the bony support is present but the cartilage tip is absent, the uncinate process is frequently described as “all bony,” but not differentiated from absent in the cladistic analysis (Appendix).
- In acanthomorphs an uncinate process is fre-

quently present on Eb1, usually well medial to the lateral end of the bone, and in percomorphs it often articulates with the lateral end of IAC. A cartilage-tipped uncinate process that articulates with Pb3 may also be present on Eb2, but it appears to be restricted mainly to some pre-acanthomorphs. Among the Acanthomorpha, an Eb2 uncinate process has evolved independently in *Hemiramphus* (Hemiramphidae, in which the process does not articulate with another skeletal element), and, variably, in *Pholidichthys* (Pholidichthyidae), in which it articulates with Pb2. Rosen and Patterson (1990:figs. 49c, 50c), probably erroneously, illustrated a posteriorly directed Eb2 uncinate process in the acanthomorph genera *Peprilus* (Stromateidae) and *Trichiurus* (Trichiuridae). We have examined a cleared and stained *T. lepturus* and find that it has a bony process on Eb2, to which LE2 probably inserts, the usual condition in acanthomorphs. Many cichlids have a separate, expanded cartilaginous process on the anteromedial edge of Eb2 which extends anteriorly ventral to Eb1, and which we do not consider to be an uncinate process.

An uncinate process on Eb3 appears first in osteoglossomorphs (*Hiodon*) followed by one on Eb4 in elopiforms (*Megalops*). Tightly juxtaposed uncinate processes on Eb3 and Eb4 are first present in some aulopiforms, but appear to be an acanthomorph synapomorphy, with occasional reversions.

The acanthomorph Eb4 levator process is usually lateral or posterior to and well separated from the uncinate process. LE4 may insert directly on the levator process or close to it. When only one process, uncinate or levator, is present on Eb4, there is a problem in deciding which it is. If the process is tightly joined to the Eb3 uncinate process, there is usually little question that it is an uncinate process. If the process is well separated from the Eb3 uncinate process, it is usually not possible to decide, unless LE4 or LP inserts on it, in which case it almost certainly is the levator process (among acanthomorphs, LE4 inserts on the uncinate process only in a few lampridiforms).

The uncinate process is absent in nemipterids, and “in *Lethrinus* and *Gnathodentex* [both Lethrinidae] it . . . has become closely associated with the levator process . . . and has lost a close association with the uncinate process of the third epibranchial” (Carpenter and Johnson, 2002:120). Early ontogenetic stages, therefore, may also offer a solution to the problem of identification of a cartilage-tipped process on Eb4 when only one such process is present.

UP—upper pharyngeal tooth plate, e.g., UP4, UP5.

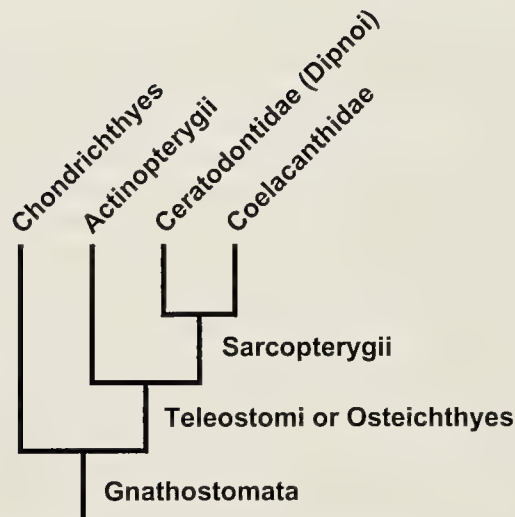


Fig. 2. Cladogram of major groups of extant Gnathostomatan fishes (derived essentially from Nelson, 1994:inside front cover) treated in the present study.

Classification

The classifications of fishes followed in our study are given in Figs. 2–4. For the most part, these are compilations of current hypotheses of relationships from which the fossil taxa have been removed. The cladogram in Fig. 2 presents the entire higher classification of taxa that include organisms generally called fishes. Fig. 3 illustrates the classification of the Actinopterygii we examined, but provides detailed branching only for the pre-Acanthomorpha. The acanthomorph classification (Fig. 4) details the major primitive clades, but generalizes the terminal clade, Percomorpha; see also Footnote 1, page 18).

The following discussion briefly examines the literature or other information on which the classifications are based.

The classification of the recent Gnathostomata in Fig. 2 derives essentially from Nelson (1994), and is generally accepted in some form (usually with more detail) in most, if not all, current general classifications of fishes (e.g., Long 1995:27, Maisey 1996:11, Gill and Mooi 2002:19).

Pre-acanthomorph classification.—The five basalmost clades of the Actinopterygii (Cladistia, Actinopteri, Neopterygii, Halecostomi, and Teleostei) and their inter-relationships that we follow were first hypothesized by Patterson (1982:253; *N.B.*, most recent authors overlook this reference, in which Patterson first included the Cladistia in the Actinopterygii, and placed it as the basalmost clade). Patterson (1994), who did not cite his 1982 study, concluded that the fossil, anatomical (extant taxa), and molecular evidence supporting monophyly of the Actinopteri conflicts, and that the Actinopteri must be considered to comprise a polytomy of Ginglimodi, Halecomorphi, and Teleostei. The anatomical evidence (Patterson

1994:68) based on extant taxa, however, supported his earlier (1982) hypothesized relationships: (Ginglimodi (Halecomorphi, Teleostei)), which we employ. Gardiner et al. (1996) reported a similar conflict, with morphological characters (including those of fossils) indicating that Ginglimodi and Halecomorphi are paraphyletic and molecular characters indicating that they are monophyletic.

There are two main opposing classifications for the basal clades of the Teleostei. Patterson and Rosen (1977) hypothesized the arrangement that we use in our cladogram. Arratia (1999) provided a radically different set of inter-relationships. Arratia based her hypothesis on 14 extant and 34 fossil taxa, using 196 characters, of which only three (her character numbers 165, 167, 190) can be considered as non-osteological. Character number 165, presence of adipose fin, appears only as a synapomorphy for two recent salmonids; 167, coiling direction of intestine, appears only as a synapomorphy for two recent osteoglossomorphs; and 190, presence of nasal sacs, supports monophyly of 12 of the 14 extant taxa and 12 of the 14 fossil taxa she examined (excludes *Amia* and *Lepisosteus*) and also supports monophyly of *Esox* and *Umbra*, the only two esociforms she examined. The major difference between Arratia's classification and that in our Fig. 3, is that her *Elops* and *Megalops* replace the Osteoglossomorpha as the sister group of all other teleosts, and the osteoglossomorphs are made the sister group of the remaining teleosts. (For possible evidence of a closer relationship of Osteoglossomorpha to Elopomorpha, see “bilaterally paired Pb muscles” in Results section of pre-acanthomorphs. For possible evidence for support of a closer relationship of Osteoglossomorpha to Clupeomorpha see discussion of Eb5 and Eb4 in “Muscles and Skeletal Elements.”)

The classification of the Osteoglossomorpha is extracted from Taverne (1998:figs. 21–22; timing precluded accommodation of Hilton's (2003) rearrangement of the taxa in our Osteoglossiformes). The Elopomorpha is slightly modified from Forey et al. (1996:fig. 2) to make the Anguilliformes a polytomy. Forey et al. studied only the Anguillidae of the three anguilliform families we include. There is little support available for the sister group of the Elopiformes, comprising the Albuliformes, Notacanthiformes, and Anguilliformes. Nelson (1973:347) proposed Anguillomorpha for this group (noted as a new super-order only in the combined index of Greenwood et al., 1973:520).

The branchings of Clupeocephala into Otocephala and Euteleostei, of Otocephala into Ostariophysi and Clupeomorpha, of Euteleostei into Neognathi and Protacanthopterygii, of Neognathi into Neoteleostei and Esociformes, and all the branches of the Protacanthopterygii (Argentiformes, Salmoniformes, Os-

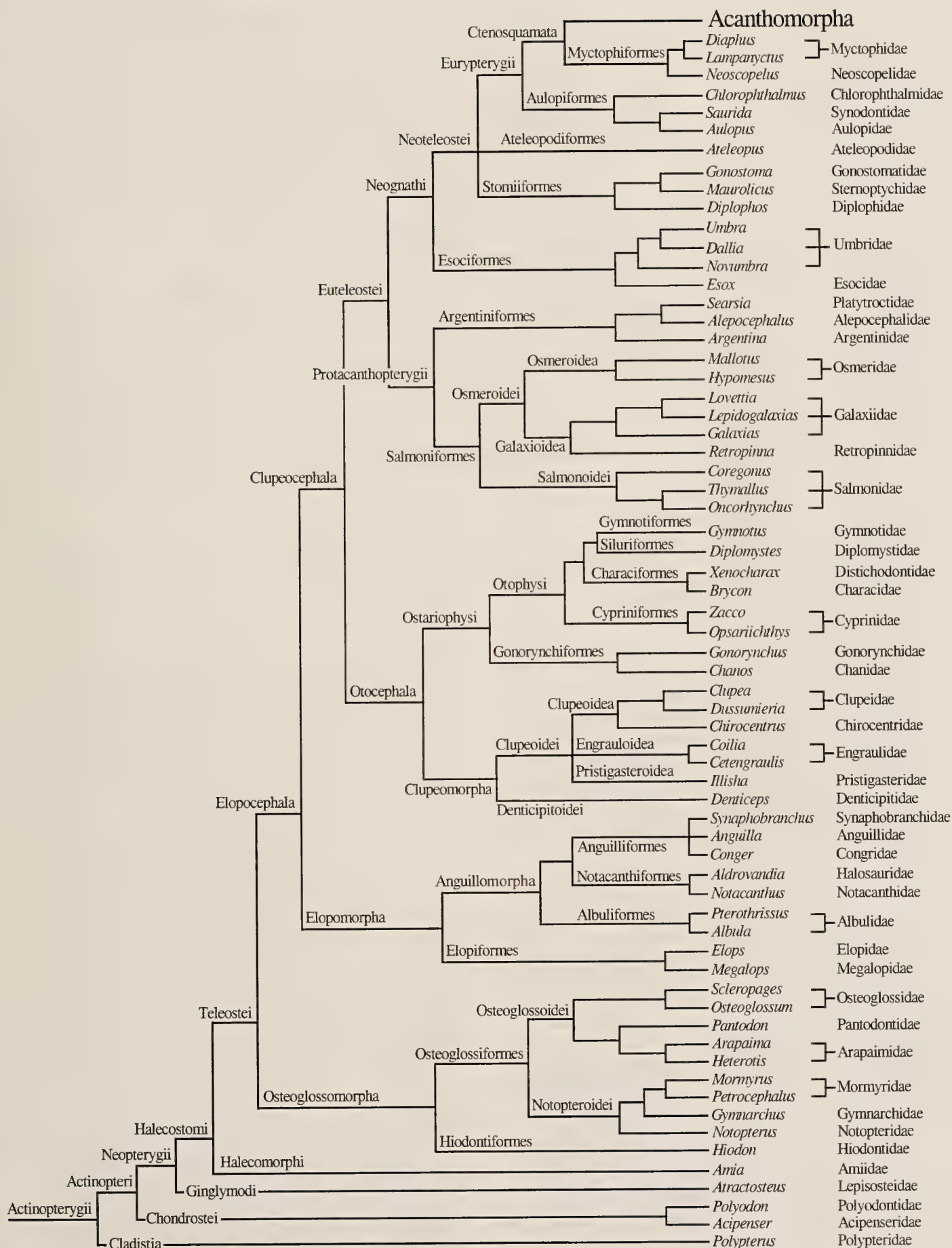


Fig. 3. Cladogram of the Actinopterygii (compiled from literature) with particular reference to pre-Acanthomorpha included in present study.

meroidei, Salmonoidei, Osmerioidea, Galaxioidea) are from Johnson and Patterson (1996:315–316). The branching of the Esociformes is taken from Nelson (1972:25) and Wilson and Veilleux (1982) and supported by Johnson and Patterson (1996:314) and Sanford (2000:214, 218, 219). López et al. (2000), based on molecular evidence, however, arrived at a different set of relationships: (*Umbra* (*Dallia* (*Esox*, *Novumbra*))).

The branching of the Clupeomorpha. Greenwood (1968) hypothesized Denticipitoidei as the sister group of the Clupeoidei (= all other Clupeomorpha), and its position has persisted to the present. The unresolved trichotomy of the Clupeoidei (Clupeoidea, Engrauloidea, Pristigasteroidea) was last hypothesized by Grande (1985). The branching of the Ostarophysi was hypothesized by Fink and Fink (1996:210–211).

With the exception of the monofamilial Ateleopodiformes, the branching of Neoteleostei to Acanthomorpha was first proposed by Rosen (1973). Rosen included the ateleopodiforms as acanthomorphs, but Olney et al. (1993:155) demonstrated they are not acanthomorphs and placed them as an unresolved trichotomy with Eurypterygii and Stomiiformes. The stomiiform branches were hypothesized by Harold (1998:fig. 4). The aulopiform branches were hypothesized by Baldwin and Johnson (1996:359).

Acanthomorpha classification.—The general arrangement of the higher acanthomorph groups is that of Johnson and Patterson (1993:fig. 24; modified slightly in our Fig. 4). We arbitrarily recognize many groups of families included in their Percomorpha as separate branches (with unresolved interrelationships) of a polytomous Percomorpha bush, which includes a polyphyletic Perciformes and polytomous Smegmamorpha as one of its several branches. Currently, there is no basis for separating Percomorpha from Perciformes.¹

¹ Johnson and Patterson (1993:591–592), in an attempt to conserve the names Percomorpha and Perciformes, defined a monophyletic Percomorpha as a clade including, among other groups, the Perciformes. They illustrated their conclusions in their fig. 11b (polychotomous smegmamorphs as sister group of Perciformes), fig. 18 right (polychotomous Smegmamorpha as sister group of a polychotomy comprising Dactylopteriformes, Scorpaeniformes, Perciformes, Pleuronectiformes, Tetraodontiformes), and fig. 24 (monophyletic Percomorpha comprising two clades, Smegmamorpha and “Perciformes, etc.” To summarize in their own words . . . we know of no sound characters justifying a pre-perciform position for Scorpaeniformes, and this emphasizes the tenuity of the distinction between our Smegmamorpha . . . and the Perciformes . . . This raises the embarrassing or mortifying possibility that we should wind up a volume on percomorph phylogeny by concluding that the group does not exist. The alternative is to save the Percomorpha by expanding it to include fishes that were originally excluded from it, the atherinomorphs. We believe that there is a monophyletic group comprising “perciforms and their immediate relatives” and our smegmamorphs. That group can be character-

Gnathostomata

(= Chondrichthyes + Telostomi)

Telostomi

(= Sarcopterygii + Actinopterygii)

Remarks. Gill-arch levators are absent in Chondrichthyes (Edgeworth, 1935:140, = his Elasmobranchii; Greenwood and Lauder, 1981:222), but are present in basal Sarcopterygii and Actinopterygii; therefore, the presence of levators is a synapomorphy of the Teleostomi.

Sarcopterygii

(= Coelacanthidae + Dipnoi)

COELACANTHIDAE

Latimeria chalumnae Smith.

Remarks. Information on *Latimeria* is based here primarily on that reported by Millot and Anthony (1958), translated a bit freely from the original French. Muscle-bone abbreviations and remarks are ours.

Description.

LE1 originates as fibers on apex of the *processus post-oticus*, near point of articulation of Pb1, and [continues] along posterior three-fourths of exterior border of Pb1.

Remarks. Nelson (1968b:fig. 5A) interpreted Millot and Anthony's Pb1 as a probable fusion of Pb1 and SPb1, but he (1969b:487 and fig. 1) later indicated it as “PH1” (= Pb1), noting that the Pbs of *Latimeria* “are difficult to compare with those of other fishes.” Evidence possibly supporting the element as either Pb1 or Pb1+SPb1 is that LE1 attaches to Pb1 in the basalmost actinopterygian, *Polypterus*, and to SPb1 in the relatively plesiomorphic *Acipenser*, Chondrostei. Unfortunately, the basalmost extant dipnoan, *Neoceratodus*, lacks both Pbs and SPbs. Nelson (1968b:fig. 5a, 1969b:fig. 1) interpreted Millot and Anthony's Pb2 as SPb2, their Eb2 as Pb2, and their Eb4+5 as Eb4.

LE2, LE3, LE4 fuse at their cranial origin, which occupies the posterior surface of the *processus post-oticus* and extends to inferior border of the supratemporal. LE2 insertion begins on posterior extremity of Pb2 [= Nelson's SPb2; see remarks following description of LE1]. It soon divides and ends capping the posterior epiphysis of Cb2. LE3 and LE4 are unit-

ized by a series of apomorphies . . . and we propose to name it Percomorpha. Johnson and Patterson, could not offer support for a monophyletic “Perciformes, etc.” and their Smegmamorpha should have been treated as just another “immediate relative” of the “Perciformes etc.” polychotomy. Nelson (1994:253) failed to note this discrepancy when he essentially reproduced Johnson and Patterson's fig. 18 right, as well as taking unexplained, although probably correct, issue with the monophyly of the Smegmamorpha.

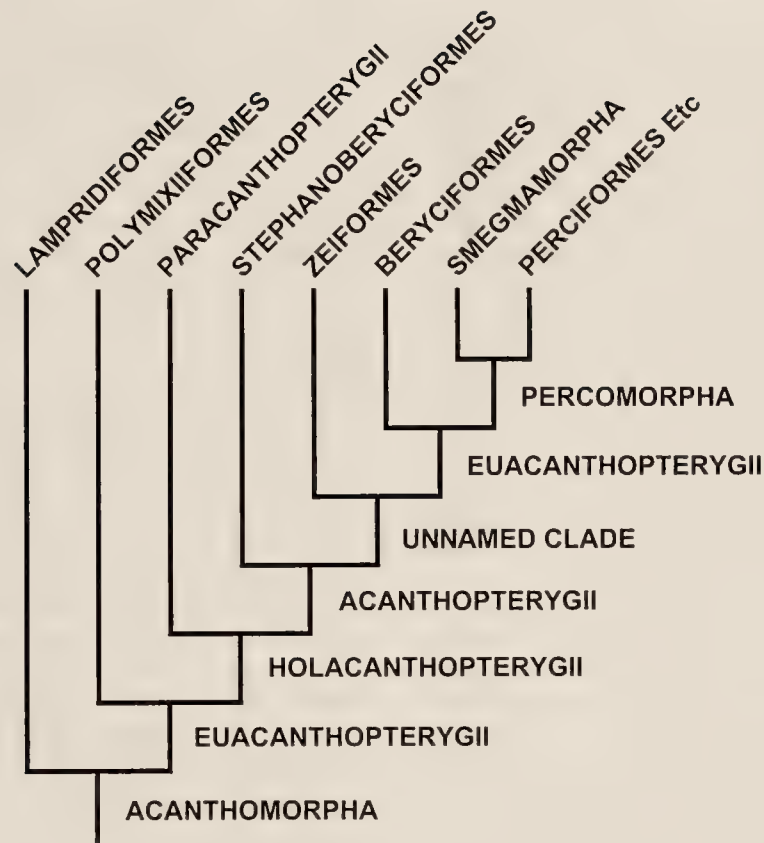


Fig. 4. Cladogram of major groups of Acanthomorpha (modified from Johnson & Patterson (1993:fig. 24).

ed as a bulky fleshy body obliquely inclined poster-oventrally. Near their movable insertions, the fibers divide and extend separately to posterior epiphyses of Cb3 and Cb4.

LE5 is noticeable for its restricted mass and attachments. It originates as three weak tendons on external surface of anocleithrum. The three tendons continue as brushlike muscles, fusing into a small, transversely flat muscle, which extends anteroventrally toward the posterior end of Cb5, to which it is attached only by very poorly differentiated fibrous tissue.

Remarks. The origin of this muscle on a cleithral element and its insertion on Cb5 suggest that it is probably homologous with PP (which Millot and Anthony do not mention) in Dipnoi and Actinopterygii. It does not appear to be homologous with LE5 of *Neoceratodus* (Dipnoi), which originates on the cranium and inserts in the dorsal esophageal CT just posterior to the gill arches.

Millot et al. (1978) expanded on the anatomy of *Latimeria*. They (1978:fig. 7; plate 22) provided a drawing and photograph of a cross-section through the gill arches. They did not mention the presence of any muscles, but clearly, there were no M. Intrbs present in the illustrations. The absence of M. Intrbs in *Latimeria* is an indication that their absences in

Actinopterygii and Coelacanthidae represent independent losses (homoplasies).

Ads absent.

SO composition unrecorded.

Remarks. Millot and Anthony (1958) do not mention which SO muscle layers are present, but Millot et al. (1978:plate 4), without comment about the muscle layers, provided a cross section of the esophagus, which indicates only a single (transverse or circular) muscle layer.

RDs absent.

Dipnoi

Remarks. Only the generally considered least specialized family, Ceratodontidae, is discussed below.

CERATODONTIDAE

Neoceratodus forsteri (Krefft), AMS I.40438001, 200 mm TL.

Plates 1.1, 1.2

Description.

LE1 mainly on dorsoposterolateralmost surface of Cb1 with very minor tendinous attachment extending from ventromedialmost edge of muscle to Eb1 dorsoposterolaterally. See remarks following LE4.

LE2 on posterolateral edge of Eb2-Cb2 joint. See remarks following LE4.

LE3 originates with LE4 and M. Intrbr3 on cranium; inserts on posterolateral edge of Eb3-Cb3 joint. See remarks following LE4.

LE4 originates with LE3 and M. Intrb3 on cranium; inserts on posterolateral edge of Eb4-Cb4 joint.

Remarks. LE1–4 are all relatively short and, according to Edgeworth (1935:129) and Fox (1965:490), who studied larvae, originate separately on the ventral surface of the auditory capsule. Greenwood and Lauder (1981:fig. 2) illustrated LE3 and LE4 originating from a common stalk. Fox (1965:fig. 8), based on a 34.5 mm larva (his largest specimen), illustrated the first three levators as originating separately from the others, and the fourth as originating with a muscle he recognized as the 6th levator, which we believe is PP.

Fürbringer (1904:489) described the insertions of the four anteriormost levators as follows (translated from German, substituting our muscle terminology): LE1 on Cb1 and posterior end of Eb1. LE2 with approximately equal parts on Cb2 and posterior border of Eb2. LE3 and LE4 insertions reduced to a minimum on [their respective] Cbs; insertions are almost exclusively on posterior border of [their respective] Ebs. Edgeworth (1935:129) described them as inserting “into the dorsal ends of the lower segments of the [branchial] bars,” and Fox (1965:490), essentially agreed, “insert on the tops of ceratobranchiale 1–4, respectively, laterally to the epibranchiale.”

LE5 originates on the ventrolateral surface of the auditory capsule posterior to the origin of LE4, and, superficially, appears to be an anterior continuation of the PP origin. LE5 has a distinct, moderately long, tendinous stem that inserts into the non-musculous esophageal tissue, where that tissue first constricts posterior to the branchial arches, and at the dorsoanterior edge of the muscular SO. At the LE5 insertion, SO is continuous only around the ventral surface of the esophageal tissue. LE5 can be considered to be closely associated with Cb5 only by a few fine, tendinous strands extending from the tendinous stem of the right-side LE5 to the PP in the vicinity of the posterior end of Cb5.

Remarks. Fürbringer (1904) and Edgeworth (1935) recognized only four LEs in *Neoceratodus*, whereas Fox (1965) recognized six. We are uncertain as to the exact homologies of Fox's LE5 and LE6. Fox (1965:490) stated that, “Levators 5 and 6, which behind merge ventrally with the coracobranchialis and posterior transversus musculature, may include a portion homologous with the dilator laryngeus and the beginning of the cucullaris muscle [= our PP] . . .” Fox (1965:fig 7) indicated the presence of only LE5 in his larval 27 mm specimen, in which it is quite long. Dorsally it closely approaches or attaches to the pos-

terior surface of the auditory capsule; anteriorly at mid-length, it closely approaches or attaches to the posterior (or distal) end of Cb5; posteroventrally it is free, but clearly directed toward the clavicle or cleithrum. In a 20 mm specimen, Edgeworth (1935:figs. 43 and 43a) labels this muscle constrictor branchialis 5 and shows it extending toward the clavicle and impinging on, or fusing with, coracobranchialis 5 posteriorly before attaching to the clavicle. In Fox's next, and last, stage larva, 34.5 mm, LE5 is no longer in contact with the cranium, having lost much of its dorsal extent, but maintaining its mid-length attachment to the distal end of Cb5. It lies along (fuses with?) the anterior or anterolateral surface of a very large LE6, which makes its first appearance and more-or-less duplicates the relative length and position of LE5 in Fox's 27 mm larva. As Fox suggested, LE6 probably represents an early stage in the formation of the PP, but unless LE5 loses its identity and fuses with PP in specimens larger than our 200 mm specimen, we do not believe it is part of PP.

PP originates on ventrolateral surface of the auditory capsule beginning musculously as an apparent, narrow, posteriorly continuous extension of the LE5 origin, but the origin becomes tendinous posteriorly; PP rapidly expands, becoming fan-like as it extends ventrally, attaching anteriorly along posterior (or lateral) border of Cb5, and reaching ventrally to the subarcualis rectus on Cb5 (Edgeworth, 1935:fig. 43b; Wiley, 1979:fig. 3c) and coracobranchialis 4 on Cb5 (Edgeworth, 1935:fig. 43b); posteroventrally, it inserts broadly on clavicle with and posterior to the coracobranchiales. (See remarks following LE5.)

M. Intrb1–4 origins are about same size as those of LEs. Intrb1 and 2 originate on cranium near origins of LE1 and 2; Intrb3 originates together with combined origins of LE3 and 4; Intrb4 originates posterior to the previous. Ventral to their origins, the fibers of each M. Intrb gradually separate in a single plane on the branchial septum, ultimately branching into about 8 filaments, each of which is separated from an adjacent filament by a narrow space; each muscle arches posteriorly, then ventrally; the filaments re-unite anteroventrally and attenuate, finally continuing anteriorly as a long, fine tendon, which inserts in CT near the anteroventral end of each muscle's respective Cb.

Remarks. M. Intrbs are known only in lungfish and elasmobranchs; thus constituting a possible synapomorphy contra-indicating a sister-group relationship between lungfish and sarcopterygians.

PrO levator-like, oriented almost horizontally, originating on ventral surface of cranium a little medial to medial end of Eb4, extending posteromedially, and inserting on non-musculous esophageal tissue posterior to branchial arches.

Remarks. We have not found this muscle men-

tioned in previous studies; it is tempting to interpret it as another form of RD, which otherwise makes its first appearance in basal Neopterygii.

SO consists only of transverse muscle layer.

Ads absent.

RDs absent (but see remarks following Pro).

Additional remarks. Huxley (1876:27) illustrated the gill arches of *Neoceratodus*. On page 37 he described them, recognizing anterior and posterior unpaired “mesobranchials” and another cartilage: “close to the ventral end of the fifth arch [= Cb5], was a small nodule of cartilage, which is probably a rudimentary sixth arch . . .” In our specimen, we found the anterior mesobranchial, which lies medially between the ventral ends of Cb2 and Cb3 on each side. Huxley illustrated its position as extending anteriorly from the ventral end of Cb2 to a point anterior to the ventral end of Cb1. His mesobranchial 1 is undoubtedly a basibranchial.

On only the right side of our specimen there is an unpaired cartilage between the ventral ends of Cb3 and Cb4. On the left side of our specimen, the ventral end of Cb5 appears to have become deeply notched sub-terminally, but continuous posteriorly with the remainder of the Cb. A small autogenous plug of cartilage fills the gap between the two continuous parts. It appears that ventral fragmentation of the Cbs may be common in *Neoceratodus*.

Actinopterygii

Pre-Acanthomorpha (Cladistia—Myctophiformes)

Cladistia

POLYPTERIDAE

Polypterus ornatipinnis Boulenger, USNM 164514,
170 mm TL.

Plate 2

Description.

LE1 on dorsoposterior edge of Pb1 and lateral portion of mostly cartilaginous Eb1 (small ossification center present in each Eb1).

Remarks. The only actinopterygians in which a levator inserts in whole or in part on Pb1 are *Polypterus* and some osteoglossiforms (*Petrocephalus*, *Osteoglossum*, *Scleropages*).

LE2 on dorsolateral surface of cartilaginous Eb2.

LE3 on dorsal surface of cartilaginous Eb3.

LE4 ventromedially on CT just lateral to SO, ventrolaterally on cartilaginous distal end of Cb4 and greatly reduced cartilage, which is here designated Eb4, and ventroanteriorly on distal end of Eb3 (see additional remarks at end of description).

LP absent.

LI1–3 absent.

TD absent; SO joined dorsally to gill arches by CT, possibly resulting from loss or extreme reduction of Eb4. (TD is also absent in Dipnoi and probably coelacanthos.)

OD3 and OD4 absent (OD first appears in Neopterygii, Ginglymodi).

OP absent, possibly concomitant with loss of Cb5.

Ad1–3 and Ad5 absent.

Remarks. If it was present in early polypterid phylogeny, Ad5, which normally attaches Cb5 to the fourth arch, was probably lost with the loss of Cb5 (see also additional remarks).

Ad4 is questionably represented by muscle joining distal end of Cb4 and reduced Eb4 with distal end of Eb3; muscle is adjacent to and questionably continuous with LE4.

Remarks. Ad4 normally attaches Eb4 to Cb4 in other actinopterygians, but with the considerable reduction of Eb4, Ad4 may have shifted its dorsal attachment to Eb3. The presence of Ads, which are absent in Chondrichthyes and Sarcopterygii (Dipnoi + Coelacanthidae), is a synapomorphy of the Actinopterygii.

RD absent.

SO longitudinal muscle layer absent.

Remarks. SO comprises a single (circular or transverse) muscle layer. SO extends anterodorsally only to a dorsally projected horizontal joining the distal ends of Cb4s. As noted by Edgeworth (1935:167), SO in *Polypterus* “does not attach to any branchial bars,” and as such, is unique among the Actinopterygii. Similar conditions pertaining to SO exist in the primitive dipnoan, *Neoceratodus*, in which, however, SO begins relatively even more posteriorly.

Additional remarks. SCL absent, TV4 absent. Prominent ligament, originating on parasphenoid, inserts on distal end of Cb1.

Jollie (1984:fig. 17b) illustrated the gill arches of *Polypterus*, purportedly based on Allis (1922:pl. 8, fig. 17b). Jollie, however, greatly increased the length of the ventral cartilaginous portion of Allis’s Eb1, interpreted the cartilage as Eb1, and labeled the two bony arms extending dorsally from the cartilage as “SPb” and “IPb.” We believe Jollie’s changes were unwarranted.

Polypterus is unusual in having only four gill arches. Britz and Johnson (2003) discuss the two hypotheses concerning the homology of the missing arch (whether it is the fourth or fifth) and strongly support the argument that the missing arch comprises the fifth ceratobranchials.

Allis (1922:232 et seq.) reported that: the first gill arch comprises Pb1 (which articulates with Eb1) Eb1, Cb1, and Hb1; the second arch comprises Pb2 with a fused, reduced Eb2, Cb2, and Hb2; the third arch comprises Pb3 with a fused, reduced Eb3, Cb3, and Hb3; the fourth arch comprises only Cb4. We agree

with Allis on the composition of arch 1 and arch 4, considering that the vestigial Eb4 is variably absent. For arches 2 and 3, we recognize Allis's Pbs as Ebs; for arch 4, the vestigial Eb4 may be absent or easily overlooked, Allis gave no evidence for his assumption that fusion had occurred between an Eb and a Pb.

Allis (1922:233) mentioned that an autogenous bit of cartilage is interposed between the [first] epibranchial and ceratobranchial of some specimens, but not others. This cartilage was also reported by van Wijhe (1882:257 and pl. 5, fig. 7), who identified it as an epibranchial, but which we term an accessory cartilage (AC). The AC (Plate 2A) is present in our specimen, and in an 85 mm SL cleared and stained specimen of *Polypterus senegalus* Cuvier (USNM 229760), but not in a 132 mm SL specimen from the same lot. The smaller of the two specimens also has an AC on the third arch of one side. We note that accessory cartilages are also present on the first and second arches of the lepisosteid *Atractosteus* (Plate 5A).

Neither Allis nor van Wijhe, noted another, small, autogenous cartilage attached to the distal end of Cb4 (Plate 2B), which is present in *P. ornatipinnis* and the smaller, but not larger, specimen of *P. senegalus*. Although Britz and Johnson (2003:499) noted the presence of this cartilage they refrained from identifying it. They cite literature in which the element has been identified variously as Eb4 or an epipharyngo-branchial.

Wiley (1979:161) discussed the homologies of the pharyngoclaviculars (PCs) in actinopterygians. He noted that polypterids, chondrosteans, and gars, which compose the pre-halecostomes, have a single PC and that halecostomes have PCI and PCE. Allis (1922:259) described PC in *Polypterus* as having a single origin on the cleithrum, but dividing into two parts with separate insertions, which he did not name, on Cb4, and which Wiley did not equate with the halecostome PCI and PCE. One can infer from Wiley's discussion, however, that the PCs (or divisions thereof) of the pre-halecostomes could be homologous with the halecostome PCI. We assign PCp to the more posterior insertion and PCa to the well-separated more anterior insertion of PC in *Polypterus*.

Wiley's hypothesis that [no portion of] the pre-halecostome PC is homologous with PCE of halecostomes, is based on two considerations. First, Wiley (1979:161) credits Edgeworth (1911) with finding that PCs are derived from the circular [our transverse] muscle layer of the oesophagus (among actinopterygians, Edgeworth's work is based on the pre-halecostomes *Polypterus*, *Acipenser*, *Lepisosteus*, and the halecostome *Amia*; Wiley accepted the presence of PCI and PCE in *Amia*). Second, Wiley dissected the halecostome *Hiodon*, which has PCI and PCE,

and found that the muscle fibers of PCE are continuous with SO longitudinal fibers. He postulated therefrom, that the PCE of halecostomes could not be homologous with the PC of pre-halecostomes, putatively derived from the SO circular layer.

We cannot find any indication that Edgeworth (1911), who studied the development of PCs, reported that they are derived from the SO circular muscle layer. In fact, Edgeworth (1911:232) concluded that "the coraco-branchiales [= our pharyngoclaviculars] of Elasmobranchs, Teleostomi, and Dipnoi . . . are derived from the ventral end of one or more branchial myotomes, i.e., are of cranial origin." Edgeworth (1935:155) reaffirmed his earlier finding, stating that in Dipnoi and Teleostomi (he modified his earlier finding for elasmobranchs), "they are developed from the outer ends of the Transversi ventrales just after these have grown inwards from the ventral ends of the branchial muscle-plates." Even so, Wiley's hypothesis that PCE of *Hiodon* (and other Teleostei) is not homologous with PCE of *Polypterus* is probably viable. Pre-halecostomes lack the SO longitudinal layer (the layer is a synapomorphy of halecostomes, see Results section following pre-acanthomorph section of this study), so that any muscle derived from the halecostome SO longitudinal muscle layer cannot have a homologue in a pre-halecostome.

Chondrostei

ACIPENSERIDAE

Acipenser ruthenus Linnaeus, USNM 62372, ca. 260 mm TL.

Plate 3

Description.

Remarks. Muscles are complex, difficult to characterize, generally not so discrete as we describe. It is possible that considerable intraspecific variation occurs; however, there was essential agreement between the right and left sides of our specimen. Marinelli and Strenger (1973:fig. 24) present a lateral view of the gill-arch musculature of *A. ruthenus* that agrees with our illustration (Plate 3B), insofar as the muscles they illustrate (they do not present a dorsal view of this musculature).

LE1 ventrally on Eb1, dorsoanteriorly on SPb1 and cranium; broad raphe on medial surface joined by anterior end of M. SPb2-LE1.

LE2 complex, comprising five parts:

M. SPb2-Eb2 on SPb2 ventrolaterally and Eb2 dorsally.

M. SPb2L origin on cranium, insertion on SPb2 dorsoanteriorly.

M. SPb2Ma origin on cranium, insertion anteriorly on mid-medial surface of SPb2.

M. SPb2Mp origin on cranium, insertion posteriorly on mid-medial surface of SPb2 and raphe with anteromedial fibers of LE3.

M. SPb2-LE1 origin from CT on medial surface of LE1, insertion anteriorly on mid-medial surface of SPb2 ventral to SPb2Ma.

LE3 origin dorsally on cranium and SPb2 posterior surface; insertion on dorsal surface of Eb3; lateral-most fibers of left LE3 continuous with fibers of RecD4 (aberrant?).

LE4 on Eb4 lateral to and continuous with RecD4 posterolaterally.

LP absent.

LI1–3 absent.

TD represented by TEb4, which is posteromedially continuous with SO.

OD3 and OD4 absent.

OP absent.

RecD4 joins dorsolateral surfaces of Eb3 and Eb4, continuous with LE4 ventrally.

Ad1–3 absent (see remarks following Ad4).

Ad4 on Eb4 dorsoposteriorly and Cb4 posteriorly, continuous ventromedially with SO.

Remarks. Edgeworth (1935:131) reported that Ad1–4 are present in *A. sturio*, but that only Ad4 is present in *A. ruthenus*, *A. fulvescens*, and *Scaphirhynchus*.

Ad5 dorsally on lateral process at distal end of Cb4, ventrally on Cb5 distal end.

RD absent.

SO comprises only transverse muscle layer.

Remarks. Wiley (1976:30–32) reported that there are two muscle layers lining the buccal cavity of *Polyodon* and *Acipenser*, an inner longitudinal layer overlain by a circular layer, and that these layers are undifferentiated from the same muscle layers lining the esophagus. We have examined both genera and find there is no muscle dorsally in the area between the gill arches. The SO in *Acipenser* and *Polyodon* comprises a single muscle layer: circular (or transverse).

Additional remarks. SCL absent. TV4 absent.

Edgeworth (1935:129) stated that constrictor branchiales (also known as interbranchiales in elasmobranchs (Daniel, 1934:105–106, 149) and lungfishes (Fürbringer 1904:488) are present in acipenserids. He (1935:130) described these as “narrow muscle bands external to the [epibranchials and ceratobranchials]. In adult stages they lie in shallow grooves in the epi- and kerato-branchialia. In *Acipenser* their ventral ends run into the outer ends of the Obliqui ventralis i, ii and iii and Transversus ventralis iv. In *Scaphirhynchus* they are overlapped by the outer end of these muscles.” Edgeworth (1935:figs. 224b and 231) illustrated these putative muscles in a sagittal section of a 32 mm specimen of *A. ruthenus* and in a ventral view of the branchial muscles and arches of *Scaphirhynchus*

phirhynchus platyrhynchus [= *S. platyrhynchus*], size not given. We did not find the muscles in *A. ruthenus* (a second specimen, USNM 64607, 295 mm TL was examined for these muscles), and they were neither reported nor illustrated by Marinelli and Strenger (1973) in their comprehensive anatomical study of *A. ruthenus*. We found only nerves and blood vessels coursing along the grooves of the epi- and ceratobranchials (see also Marinelli and Strenger, 1973: fig. 240). We did not examine *Scaphirhynchus*.

POLYODONTIDAE

Polyodon spathula (Walbaum), USNM 101093, 217 mm TL.

Plate 4

Description.

LE1 on dorsal edge of Eb1 near medial end and by tough CT on posterior edge of SPb1.

LE2 on dorsal edge of Eb2 near medial end and by tough CT on posterior edge of SPb2.

LE3 on Eb3 uncinat process, continuous with LE4 above insertion.

LE4 on Eb4 dorsal edge somewhat distal to medial end, continuous with LE3 above insertion.

LP absent.

LI1–3 absent.

TD consists of TEb4, which is continuous and undifferentiated from SO.

OD3 and 4 absent.

OP absent.

RecD4, small, anteriorly on dorsodistal edge of Eb3, posteriorly by tendon to Eb4 at insertion of LE4.

Ad1–4, each dorsally, broadly on posterior surface of respective Eb, ventrally, narrowly on anterior surface of respective Cb just medial to inner angle formed by Eb-Cb joint.

Ad5 dorsally on ventrodistalmost surface of Eb4, ventrally on dorsal surface of Cb5.

Remarks. Edgeworth (1935:131) considered our Ad5 to be a 5th levator.

RD absent.

SO continuous with TEb4; comprises only transverse muscle layer (see remarks under SO in *Acipenser*).

Additional remarks. SCL absent. TV4 absent. Danforth (1913) described the musculature of *Polyodon*. Our findings are in essential agreement. He reported that the four levators arise from a continuous sheet and separate as they proceed toward their insertions. He worked on specimens much larger (ca. 1 m) than the one we describe, in which LE3 and LE4 are scarcely separate at their insertions. The difference noted may be ontogenetic.

Ginglymodi

LEPISOSTEIDAE

Atractosteus tropicus Gill, USNM 120715, 415 mm TL.

Plate 5

Description.

LE1 on dorsal surface of cartilaginous distal end of Eb1.

LE2 on Eb2 (both removed when gill arches were removed; position in illustration is approximate).

LE3 on dorsal surface of cartilaginous distal end of Eb3.

Remarks. Short ligament (not illustrated) extends posteriorly from base of LE3 and inserts on anterior margin of cartilaginous distal end of Eb4.

LE4 on dorsal surface of cartilaginous distal end of Eb4.

LP absent.

LI1 on dorsal bony surface of Pb2 and medial surface of SPb1.

LI2 mostly on cartilage at ventral junction (not shown) of bony and cartilaginous portions of Pb3 proximal to anteriormost Pb3 teeth.

LI3 absent (Pb4 absent).

TD comprises only TPb3, which is continuous anteriorly but originates posteromedially from raphes with SO and RDs and anastomoses ventrally with CT underlying SO. Laterally, TPb3 attaches and surrounds Pb3 dorsolateral process (see also RD) and is continuous with anterior end of OD4.

OD3 absent.

OD4 originates on dorsal end of Pb3 process and inserts along anterodorsal edge of medial end of Eb4.

OP absent or indistinguishable medially from Ad4 and/or SO. Muscle laterally in this region joins Eb4 and Cb4 medial to joint of these two elements.

Ad1–3 absent.

Ad4 absent or indistinguishable medially from OP and/or SO (see OP and Ad5).

Ad5 on posterodistal end of Cb4 and dorsodistal end of Cb5, inseparable medially from SO; some fibers on Cb4 questionably represent Ad4.

Remarks. The muscles in this area are surrounded and penetrated with tough connective tissue, and the delineation of the muscles is not as clear as they appear in Plate 5.

RD inserts anteriorly on raphe that joins SO, Pb3, and TPb3 in region at and ventral to posterior end of TPb3.

Remarks. Wiley (1976:32) stated that the RDs of lepisosteids share muscle fibers with the circular muscle layer of the esophagus [SO]. We note that SO does not have a longitudinal muscle fiber layer in *Atractosteus* and that RD fibers are not continuous with the SO circular muscle fibers, although the fibers

of both RD and SO are permeated with (joined by) anastomosing connective tissue. (See discussion of RD in Results section of pre-acanthomorphs.)

SO attaches to Pb3 anteriorly and is free from Eb4, but dorsolaterally is inseparable from OP and/or Ad4 on Eb4; comprises only transverse muscle layer.

Additional remarks. SCL absent. TV4 absent. Wiley (1976:32), erroneously reported TV4 present in lepisosteids, and concluded that its presence was a synapomorphy of the Neopterygii. His fig. 14, however, accurately shows TV4 is absent in lepisosteids. TV4 first appears in *Amia* and is a synapomorphy of the Halecostomi. Pb2 is well removed from contact with Pb3. There are two cartilaginous SPbs, one each on the uncinat processes of Eb1 and Eb2. There is a pair of wedge-shaped ACs between the anterodistal and posterodistal ends of Eb1 and Eb2 and their respective Cbs. See also references to Wiley (1976) in Additional remarks under *Amia calva*.

Halecomorphi

AMIIDAE

Amia calva Linnaeus, USNM 230909, 120 mm TL.

Plate 6

Description.

Remarks. Allis (1897) and Holstvoogd (1965) described and illustrated the dorsal gill-arch musculature of *A. calva*; however, we find the illustrations and descriptions wanting.

LE1 on dorsoposterior edge of Eb1 just lateral to proximal cartilaginous end.

LE2 on dorsomedial cartilaginous process (end) of Eb2, which articulates with Pb3 (end ventromedially articulates with Pb2).

LE3 on posteriorly extending portion of Eb3 cartilaginous medial end.

LE4 on both cartilage and bone at distal end of Eb4.

LP absent.

LI1 on anterior cartilaginous tip of Pb2.

LI2 on cartilaginous portion of Pb3 dorsal to uncoalesced tooth plates.

LI3 absent (Pb4 absent).

TD comprises only TPb3, which attaches to anterolateral portion of Pb3, with some posteromedial fibers on right side continuous with right-side RD.

OD3 absent.

OD4 relatively short; origin on anteromedial cartilaginous portion of Pb3, insertion on medial end of Eb4, posteromedially joining small raphe with dorsomedial end of OP.

OP on Eb4 dorsomedially, on Cb5 distally, continuous with SO ventromedially, overlaps ventral end of Ad5; ER absent.

Ad1–3 absent.

Ad4 on dorsoposterior surface of Eb4 and dorsal surface of Cb4.

Ad5 on distal cartilaginous ends of Cb4 and Cb5.

RD completely separate from SO; with separate dorsal and ventral attachments on Pb3 ventral to TPb3; few or no muscle fibers continuous with TPb3 on left side, several fibers continuous with TPb3 posteriorly on right side. (See discussion of RD in Results section of pre-acanthomorphs.)

SO on Pb3 posteriorly; does not attach to Eb4; longitudinal muscle fibers sparsely distributed within SO, roughly paralleling mucosal folds, extend anteriorly to posterior margins of posteriormost upper pharyngeal tooth patches.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 positioned horizontally, in line with Eb1. We agree with Wiley's (1976:30–31) conclusions, based on *Amia* and lepisosteids, which have only OD4, that TD and OD muscles are apomorphic for Neopterygii; however, OD3 is a synapomorphy of the Teleostei.

Osteoglossomorpha

HIODONTIDAE

Hiodon alosoides (Rafinesque), USNM 350554, 2 specimens, 102–130 mm.

Plate 7A, B

Additional material. ② = *Hiodon tergisus* Lesueur, USNM 266581, 82.1 mm; USNM 342742, 154 mm; USNM 350555, 163 mm.

Plate 7C

Description.

LE1 finely, tendinously on cartilaginous medial end of Eb1.

LE2 on cartilaginous medial end of Eb2.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 dorsodistally on Eb4.

Remarks. LE4 origin is well separated posteriorly from the linearly contiguous or clustered origins of the other levators. As such, LE4 in *Hiodon* could be interpreted as LP (Winterbottom, 1974b:footnote p. 252), which, in fishes with both LE4 and LP, always originates posterior to the origins of the other levators. In other osteoglossomorphs, except the highly specialized *Heterotis*, the origin of the levator inserting dorsodistally on Eb4 is linearly contiguous with the other levators, and there is no levator inserting posterior to it. Greenwood and Lauder (1981:226) opined that LE4 in *Hiodon* has been displaced posteriorly because of "the large swimbladder extension in the otic region." The interpretation of the posteriormost levator as LE4 might be contraindicated by the condition of the levators in one of the three specimens of *H. tergisus*. The disposition of the levators in two of the specimens of *H. tergisus* we examined

is similar to that of both specimens of *H. alosoides* (Plate 7A). In the third specimen of *H. tergisus* (USNM 342742), however, there is, bilaterally, a slender, additional levator tendinously inserting on Eb4 well anterior to the typical posteriorly inserting LE4 (Plate 7C). The additional muscle is probably anomalous. Our observations indicate that LP is present in pre-acanthomorphs only among some of the fishes belonging to the Otocephala (some clupeomorphs and ostariophysans), but it is usually present in acanthomorphs.

LP absent (see remarks under LE4).

LI1 on bony dorsal surface of Pb2.

LI2 (see Remarks under LI3).

LI3 (see Remarks).

Remarks. There appears to be only one other LI besides LI1. In the smaller specimen of *H. alosoides*, a few fibers of the second LI insert posteriorly on Pb3, and the remainder insert on Pb4. In the larger specimen, the second LI inserts extensively on both Pb3 (posteriorly) and Pb4 (anteriorly). In two of the three specimens of *H. tergisus*, the second LI has minor insertion posteriorly on Pb3 and the remainder on Pb4. In the third specimen, the second LI has completely separate insertions on Pb3 and Pb4, with the more extensive insertion on Pb4. It is not possible to decide if the second LI represents: LI2 inserting partially on Pb4, fused LI2 and LI3, or LI3 with partial insertion on Pb3. Nelson (1969b:18) indicated the presence of only two LIs in osteoglossomorphs, but did not specify their insertions. We find only one LI in *Petrocephalus*, *Mormyrus*, and *Gymnarchus* (LI1), and only two in *Arapaima* (LI1, LI2). *Notopterus*, *Heterotis*, *Osteoglossum*, *Scleropages*, and *Pantodon* all have three (LI1–3).

TD is broad, undifferentiated, consists of TPb3–Pb4–Eb4, continuous posteriorly with SO, from which it is differentiated only by divergence of muscle fibers at posterior attachment to Eb4.

OD2 absent. ② Present in two smaller specimens (Plate 7C) in which it is small, originates on Pb3 near posterolateral origin of OD4, and inserts jointly with LE2 on Eb2 cartilaginous medial end.

Remarks. Among pre-acanthomorphs, OD2 is otherwise known only in *Heterotis*, which, together with *Hiodon*, also lacks TEb2. The bones joined by the bilateral pair of OD2 muscles are the same as those joined by TEb2 (or TEb2 complex) of other osteoglossomorphs (*Arapaima*, *Osteoglossum*, *Scleropages*, *Pantodon*). TEb2 in these fishes, however, is a transverse muscle connecting the two sides of the gill arches. It is possible that OD2 is a modified TEb2.

OD3 origin on Pb3 lateral to and continuous with OD4 origin, insertion dorsally on Eb3 uncinat process just ventral to LE3 insertion.

OD4 origin on Pb3 medial to and continuous with OD3 origin, insertion on anteromedialmost edge of

Eb4 coincident with anterior attachments of Ad4 and OP.

RecD4 origin on Eb4 dorsally anterolateral to OD4 insertion; insertion split, dorsally on dorsoposterior surface and edge of Eb3 uncinat process and ventrally on medial end of Eb3 (not illustrated), variously fusing with LE3 basally.

Remarks. Nelson (1967a:281; 1967c) used the term *obliquus inferior* [of the dorsal gill-arch musculature] for a muscle joining two adjacent epibranchials in eels. Winterbottom (1974b:259) noted that *obliquus inferior* is a muscle of the eye and that the term also had been applied to various other muscles. He, therefore, coined the name *recti dorsales* (sing., *rectus dorsalis*) for longitudinal muscles joining adjacent epibranchials "to reflect their analogous position to that of the *recti ventrales*." RecDs occur in a diverse variety of fishes (e.g., osteoglossomorphs, anguilliforms, callionymids, etc.), and are probably homologous only within restricted groups of taxa.

OP a narrow strap, originating on posteromedial margin of Eb4 coincident with ventral portion of OD4 insertion, ending posteroventrally at ER, which is joined ventrally by Ad5 and SO; second, even slenderer portion of OP may be present, originating separately somewhat ventral to narrow portion, inserting together with narrow portion. ② Originating laterally with Ad4 attachment; not distinguishable from SO.

Remarks. Below ER, it is not possible to decide if OP is continuous laterally with Ad5 or is replaced by a medially expanded Ad5.

Ad1–3 absent.

Ad4 origin on Eb4 dorsomedially, coincident with OD4 insertion, insertion on dorsoposterior surface of Cb4.

Ad5 on Eb4 dorsoposteriorly and on Cb5 laterally, joining ER medially with SO (see also remarks under Ad5 in description of *Arapaima*).

RD absent.

SO longitudinal muscle layer thick dorsally and ventrally, thin to almost absent laterally, extends anteriorly only to horizontal at posterior margin of TPb4–Eb4.

Additional remarks. SCL absent. TV4 free from Cb5s. The distinct crossed anterior ends of Pb3s are dorsal to the crossed anterior ends of Pb2s, and the complex is completely encompassed in a ball of thick connective tissue (not shown) that attaches to the ventral surface of the cranium.

NOTOPTERIDAE

Notopterus notopterus Pallas, USNM 344674, ca. 127 mm; USNM 191464, ca. 143 mm.

Plate 8

Description.

LE1 on dorsal Eb1 bony surface just lateral to cartilaginous medial end; dorsoanteriorly, fibers on medial surface mesh with fibers on lateral surface of LE2.

LE2 dorsally on Eb2 cartilaginous and bony surfaces just lateral to joint with Pb3; dorsoanteriorly, fibers on medial surface mesh with fibers on lateral surface of LE3' and fibers on lateral surface mesh with fibers on medial surface of LE1.

LE3 on tip of Eb3 uncinat process jointly with "3" attachment of OD3–4.

LE3' on dorsal surface of medial end of Eb3; dorsoanteriorly, fibers on lateral muscle surface mesh with fibers on medial muscle surface of LE2, and fibers on medial surface mesh with fibers on lateral surface of LI3. See also "Additional remarks" below.

LE4 on cartilaginous dorsoposterior end of Eb4.

LP absent.

LI1 on bony dorsal surface of Pb2 just lateral to medial cartilaginous end.

LI2 on dorsal surfaces of Pb3 and Pb4; insertion paralleling and distinct from LI3 insertion.

LI3 on dorsal surface of cartilaginous Pb4, paralleling and distinct from portion of LI2 insertion on Pb4, also a few fibers dorsally on medial end of Eb3; dorsoanteriorly, fibers on lateral surface mesh with fibers on medial surface of LE2.

TD broad, undifferentiated, consists of TPb3–Pb4–Eb4. In smaller specimen, TD overlies and is free from anterior end of SO. In larger specimen, TD is continuous posteriorly with SO, from which it is differentiated only by divergence of muscle fibers at posterior attachment to Eb4.

OD3–4 origin on Pb3 bony portion adjacent to anterior cartilaginous tip, posteriorly muscle divides longitudinally with branch inserting on cartilaginous tip of Eb3 uncinat process and branch dorsally on cartilaginous distal end of Eb4 where it forms lateral half of raphe with dorsal end of Ad4 and is partially continuous with LE4 insertion.

OD4 origin beginning on dorsoposterior bony portion of Pb3 medial to LI2 insertion, continuing along most of length of cartilaginous Pb4, and inserting on Eb4 dorsodistally and forming medial half of raphe with Ad4.

RecD4 a sliver of muscle tendinously attached anteriorly to dorsal tip of Eb3 uncinat process; passes posteriorly between Eb4 portion of OD3–4 and OD4, conforming with surface of OD4, and joins raphe with Ad4 along with and posterior to OD4.

OP absent or fused indistinguishably with SO; ER present at about level of dorsalmost attachment of Ad5.

Ad1–3 absent.

Ad4 on EB4 dorsoposteriorly, joined there by ra-

phe with OD3–4, OD4, and RecD4; on Cb4 dorsal surface anterior to Eb4-Cb4 joint.

Ad5 on posterior cartilaginous distal end of Eb4 and posteromedial surface of Cb5, mostly undifferentiated from SO laterally.

RD absent.

SO longitudinal muscle fibers thickest dorsally, extending anteriorly to anteromedial end of Pb3.

Additional remarks. SCL absent. TV4 free from Cb5s. Holstvoogdt (1965:fig. 5) illustrated the levators of the notopterid *Xenomystus nigri*. He found only six, four of which appear to be equivalent to our LE1, LE2, LE4, and LI1. The equivalents of the other two levators, which he labels as L.III EX. and L.III.INT. are unclear, but possibly represent our LI2 and LI3, which, if true, would indicate that *Xenomystus* appears to lack LE3 and LE3'.

GYMNARCHIDAE

Gymnarchus niloticus Cuvier, USNM 319410, ca. 315 mm TL.

Plate 9

Description.

Remarks. The dorsal gill-arch musculature and skeleton are considerably reduced and muscle fusions are evident. Because of this, it is simpler to describe much of the musculature in narrative form.

The only levator that is clearly present is LI1, which is on Pb2 posteromedially. A large, long muscle, or muscle complex, probably incorporating LE1 and/or RecD1 ("LE1 complex" on Plate 9A), extends well anteriorly from the anterior edge of Eb1. The dorsal surface of the muscle attaches along the ventral surface of the cranium. A long muscle, possibly comprising LE2 anteriorly, is incorporated dorsally in the LE1 complex. As this questionable LE2 extends posteriorly, it attaches musculously to the posterior bony surface of Eb1, then tendinously to the bony surface of Eb2 (incorporating a RecD2?), continues musculously (as RecD3?) posteriorly, and forms tendinous anterior and posterior attachments to Eb3 and the anterior bony edge of Eb4. A short muscle (M. Pb3-Eb3-Eb2) connects the posteromedial bony dorsal surface of Eb2 with Pb3 and Eb3, where the latter two elements meet. Another muscle, RecD4, joins the dorsoposterior bony surface of Eb3 with the dorsal bony surface of Eb4.

TD comprises TPb2-Pb3-Eb4, originates anteriorly at about level of Pb2s as sparse fibers on surface of CT; anterolaterally, fibers appear to form part of medial edge of LE1 muscle complex. TD becomes sheet-like posteriorly beginning at about level of Pb3s, and is undifferentiated posteriorly from SO.

OD3 absent.

OD4 absent.

OP absent; presence or absence of ER unclear.

Ad1–3 absent.

Ad4 on ventral surface of Eb4 and dorsal surface of Cb4.

Ad5 dorsally attaches to tendon extending laterally from Eb4, and ventrally to posterodistal end of Cb5; a unique, laterally extending strap of SO arises from anterior surface of tendon and sandwiches Ad5 between it and another SO strap arising from Cb5 area ventrally.

RD absent.

SO longitudinal muscle layer comprising sparsely distributed fiber bundles in "cottony" matrix, extending anteriorly to anterior end of TD.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 and Pb4 are absent. Tiny AC present only on left side at posteromedial tip of Eb1.

MORMYRIDAE

Petrocephalus tenuicauda (Steindachner), USNM 118801, 92.3 mm.

Plate 10

Additional material. ② = *Mormyrus longirostris* Peters, USNM 261878, 225 mm.

Description.

LE1 on Eb1 anterior and posterior edges (bridging channel that carries blood vessels and nerves) with some fibers also on Pb1; fuses posteromedially with LE2. ② Unclear if LE2 is represented among fusions.

LE2 on Eb2 posteromedially, fuses laterally with LE1 and medially with M. Pb3-Pb4-Eb2, which may represent a modified LI2 and/or LI3. On left side, a muscle originates narrowly and separately on cranium and inserts narrowly, tendinously on Eb2 among fibers of broad, fused complex LE2. This muscle is also labeled LE2 on Plate 10. ② Unclear if LE2 is present, but if so, is incorporated in RecD2.

LE3 on all bony Eb3 uncinat process just lateral to RecD3 and OD3 attachments. ② Extremely long and variable in width along its length, changing almost to thin tendon in places.

LE4 absent.

LP absent.

LI1 on dorsomedial surface of Pb2.

LI2 see LE2.

LI3 see LE2.

M. Pb3-Pb4-Eb2 originates on posterodorsal surface of Pb3 and dorsal surface of greatly reduced Pb4, and inserts on Eb2 posteromedially; anteriorly, fuses with lateral portion of LE2. ② LE2 portion questionably present.

TD apparently undivided, consisting of TPb3-Pb4-Eb4, more-or-less continuous posteriorly with SO. ② Comprises TPb3 and questionably TPb4-TEb4. TPb3 dense band of muscle fibers attached to Pb3 dorsoanteriorly, abruptly changing posteriorly to loose

strands of diagonal muscle fibers attaching to Pb4, and these continuing posteriorly as dense network of fibers attaching to Eb4 posteromedially and continuing posteriorly as SO.

OD3 tendinously on Pb2 (rather than Pb3 as in most fishes), and tendinously on all bony Eb3 uncinat process. On right side only, there is a possibly anomalous strap of muscle extending anteriorly from Eb3 uncinat process that fuses anteriorly with LE1-LE2 complex; strap lies dorsal to M. Pb3-Pb4-Eb2.

② Strap absent.

OD4 absent.

M. Pb2-Eb1 narrowly on posteromedial edge of Eb1 (ventral to anteriorly extending, fused LI2+3? and LE2) and broadly on anterodorsal surface of Pb2.

② Originates on dorsoanterior surface of Pb3, with slender tendon on medial surface of muscle expanding anteriorly and joining CT covering Pb2-Pb3 joint.

RecD2 broadly on dorsal surface of Eb2 ventral to LE2, and narrowly on posteromedial corner of Eb1 ventral to LE2. ② Presence of LE2 questionable.

RecD3 on all bony uncinat process of Eb3 and dorsal surface of medial cartilaginous end of Eb2. ② Asymmetrical; left side with cluster of small muscles originating on Pb3, Pb4, and Eb4 medially, and inserting on Eb2 anteromedially; right side with two small muscles, one from Eb2 anteromedially to Eb4 anteromedially, the other from Eb2 anteromedially to Eb3 dorsomedially.

OP questionably present.

Remarks. ER, often denoting the ventral end of OP, when OP is present, is irregularly indicated on both sides of SO at about the level of the distal end of Eb4. On the left side there is a narrow strap of muscle that originates on Eb4 and ends at the raphe. On the right side there is no strap. ② Many raphe-like CT intrusions in SO dorsolaterally; no defined strap-like muscle; muscle fibers complexly oriented. Differences from *Petrocephalus* possibly due to much larger size of specimen.

Ad1-3 absent.

Ad4 dorsally on Eb4 dorsoanteriorly and ventrally on Cb4.

Ad5 dorsally on dorsoposterodistalmost cartilaginous tip of Eb4 and ventrally on Cb5; fuses medially with SO.

RD absent.

SO longitudinal fibers essentially restricted to dorsal arc of SO ventral to transverse fibers, few if any longitudinal fibers ventrally. ② Fibers sparsely distributed dorsally, few if any laterally or ventrally.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 is greatly reduced and offers little surface for attachment of a levator. This could explain the absence of LI3, if present ancestrally.

Bishai (1967:20-21) described and illustrated the dorsal gill-arch musculature of *Mormyrus caschive*

Linnaeus. Using terminology different from ours, he reported the presence of LE1-4, LI2 and 3 (on Pb2 and 3, respectively, which would equal our LI1 and LI2), OD3, and a muscle that we would term OD3' (the two originating on separate parts of Pb3 and inserting together on bony Eb3 uncinat process), RecD2 and 3, and Ad4. He did not mention fusion of any muscles, and his illustrations do not indicate the presence of cartilage. It is possible that his LI3 may insert partially on Pb4.

Nelson (1969b:18) reported on the dorsal gill-arch muscles of *Mormyrus ovis*, in which he recognized only LE1 and 2, LI1, OD3, OD4, and RecD 2 and 3 (no mention of Ads). Although Nelson mentioned Bishai's study, he made no comment on the differences between his findings and those of Bishai. We believe there is considerable room for differences in interpretation of the muscles, as well as the possibility that no two specimens of the same species (or two sides of a specimen) are more than generally similar. Our remarks undoubtedly also apply to our specimens of *Petrocephalus* and *Mormyrus*.

ARAPAIMIDAE

Heterotis niloticus (Cuvier), USNM 303214, 237 mm.

Plate 11

Description.

Remarks. *Heterotis* is unique among osteoglossiforms we examined in having an epibranchial organ. The organ is formed by the complex coiling and extensive development of what is probably the dorsal cartilaginous margin of Eb4, and, at least, includes that margin. The thin muscle branches attaching variously to the surface of the cartilage are difficult to homologize with reasonable certainty. Adding to the difficulty are bilateral asymmetry of these muscles, a sheet of muscles lining the internal surface of the cartilaginous coil, and an extensive network of invasive nerves supplying the organ internally and externally. We have not indicated nerves in other illustrations, but in Plate 11A, we show a large nerve (identification not determined), which superficially resembles a muscle. The nerve penetrates the dorsomedial side of the cartilaginous coil.

LE1 on cartilaginous and bony dorsomedial end of Eb1, fusing dorsally with anteroventral, longitudinal fibers of LE2. Short ligament (not illustrated) joins dorsomedial surface of cartilaginous medial end of Eb1 to bony dorsal surface of anterior end of Pb2.

LE2 on dorsalmost prominence of cartilaginous medial end of Eb2; muscle fusing ventrally with dorsal, longitudinal fibers of LE1. RecD2 parallels LE2 ventrally, with ribbon of CT (not illustrated), which connects cartilaginous processes of Eb1 and Eb2, lying laterally and attaching to both muscles. Short lig-

ament (not illustrated) joins dorsomedial surface of cartilaginous medial end of Eb2 to dorsal bony surface of anterior end of Pb3.

LE3 tendinously on cartilaginous tip of Eb3 uncinuate process; muscle thin, weak, posterodorsally directed, applied medially to lateral surface of epibranchial organ; origin not noted, but apparently not attaching directly to cranium; muscle possibly absent on right side, or lost during dissection.

LE4 on dorsal surface of epibranchial organ, conforming with curvature of organ; possibly absent on right side or lost during dissection.

LP absent.

LI1 on Pb2 mid-dorsally.

LI2 on bony Pb3 dorsal surface; right side with slender posterior branch inserting anteriorly on dorsal surface of cartilaginous Pb4; branch absent on left side.

LI3 attached to fascia covering surface of cartilaginous Pb4; anterior, elevated portion of muscle interrupted at attachment, continuing posteriorly as CT and then small portion of muscle applied to posterior surface of Pb4 (muscle uninterrupted on right side); CT at base of elevated portion gives rise to posterior attachment of M. Pb4-Eb2. LI3 passes anteriorly lateral to LI2.

TD possibly absent anteriorly (see OD2), comprises TPb3-Pb4 (on posterior Pb3 segment and, possibly, also on Eb4), and is undifferentiated posteriorly from SO.

OD2 originates on dorsal surface of autogenous cartilaginous Pb3 anterior segment (Nelson, 1968a: 268) anterior to OD3 origin, and inserts on cartilaginous medial end of Eb2 dorsally. Medial fibers of right-side OD2 overlap anterior end of left-side OD2 and attach on dorsoanterior end of left-side Pb3 cartilaginous segment. Anterior ends of Pb3 cartilaginous segments and OD2 origins are enveloped in tough CT pad.

Remarks. OD2 is known otherwise in pre-acanthomorphs only in some specimens of *Hiodon tergisus*. See remarks under OD2 in description of *Hiodon*.

OD3 originates on dorsal surface of Pb3 anterior segment and inserts by long tendon on tip of elongate cartilaginous cap of Eb3 uncinuate process. Right-side origin is ventral to OD2 origin; left-side origin begins at posterior end of OD2 origin.

OD4 absent on left side; questionably represented on right side by thin, elongate muscle originating on Pb3 just anterior and medial to LI2 insertion and inserting on posterior (= medial in view) cartilaginous wall of EO (Eb4).

OP absent; ER absent.

RecD2 on posterior surface of dorsal prominence of medial cartilaginous end of Eb1 and anterior surface of dorsal prominence of medial cartilaginous end of Eb2, parallels LE2 ventrally, with CT ribbon (not

illustrated) connecting cartilaginous processes of Eb1 and Eb2 passing laterally and attaching to both muscles. Left-side RecD2 comprises a vertical pair of muscles, each member of which attaches tendinously to Eb2; right-side RecD2 has vertical series of three separate, but contiguous muscular attachments to Eb2.

RecD3 absent.

RecD4 absent, but long, broad ligament arising from Eb3 uncinuate process and lateral edge of Pb4 inserts on dorsal bony surface of Eb4.

M. Pb4-Eb2 attaches to posterior surface of dorsomedial cartilaginous extension of medial end of Eb2 and inserts by flat tendon on Pb4 ventral to insertion of elevated portion of LI3 (q.v.).

Ad1–3 absent.

Ad4 fan-like, attaching inner cartilaginous ventro-posterolateral surface of EO (Eb4) to bony medial surface of posterior end of Cb4; dorsally, begins at lower internal rim of large foramen in anterior surface (lateral in view) of cartilaginous posterior end of Eb4 (Plate 11B) and expands anterodorsally ending as fine sheet of CT attaching to medial surface of dorsoposterior bony flange of Eb4. Large, fan-shaped gill-filament muscle (not illustrated) on posterolateral bony surface of Eb4 matches somewhat the shape of Ad4 on internal surface. On left side, an apparently anomalous slip of Ad4, which attaches dorsal to remainder of muscle, is visible through the Eb4 foramen, after removal of fine sheath of muscle lining inner wall of epibranchial organ.

Ad5 small, horizontal muscle joining posteroventral cartilaginous surface of EO (Eb4) to dorsoposterior cartilaginous surface of Cb5.

RD absent.

SO longitudinal muscle fibers questionably absent, sparse if present.

Additional remarks. SCL absent. TV4 free from Cb5s. Glottis present.

Arapaima gigas (Cuvier), USNM 177528, 2 specimens, ca. 135–139 mm.

Plate 12

Description.

LE1 on Eb1 dorsoposterior edge just lateral to medial cartilaginous end.

LE2 absent.

LE3 absent.

LE4 on dorsoposterior edge of distal cartilaginous end of Eb4.

LP absent.

LI1 on Pb2 dorsoposteriorly.

LI2 on dorsal surface of Pb3 posteromedially.

LI3 absent.

Remarks. M. Pb4-Eb2 conceivably represents LI3

that has shifted its origin to Eb2. (See also remarks under LI3 in *Hiodon*).

TD comprises two parts: TPb3-Eb2 and TPb3-Pb4-Eb4. TPb3-Eb2 a very thin sheet of muscle attaching to dorsal surface of Pb3 anterior cartilaginous segment (Nelson 1968a:267–268) and cartilaginous processes of Pb3 (posterior bony segment) and Eb2, where these processes join, and is anterodorsal to TPb3-Pb4-Eb4, which attaches to medial edges of Pb3, Pb4, and Eb4. TEb2 is dorsal to anterior attachments of OD3 and OD4. TPb3-Pb4-Eb4 is undifferentiated posteriorly from SO.

OD3 on autogenous anterior Pb3 cartilaginous segment and Eb3 uncinuate process.

OD4 anteriorly on Pb3 bony portion, posteriorly on dorsomedial edge of Eb4, fusing posteriorly with RecD4.

Remarks. Our interpretation of OD4 and RecD4 (q.v.) may be in error and the muscle we indicate as RecD4 may be the Eb3 branch of an OD3–4, a muscle otherwise limited to *Notopterus* and *Pantodon* among Osteoglossomorpha. *Pantodon* lacks a separate OD4. Only *Notopterus* among the Osteoglossomorpha has OD4, OD3–4, and RecD4, and *Notopterus* lacks OD3, which is present in all other Osteoglossomorpha except *Pantodon* and the highly specialized *Gymnarchus*, which lacks OD completely. Our general observation among Neopterygii, is that, excluding *Notopterus*, OD4 or OD3–4 may be present, but not both. Very few neopterygian taxa (*Gymnarchus*; the ostariophysan *Chanos*) lack an OD, a lack we consider autapomorphic for each of these taxa.

OP absent; ER absent.

Remarks. There is considerable CT permeating and obscuring the nature of the area that might be defined as OP.

RecD2 on cartilaginous posterior edge of Eb1 medial end and bony posterior edge of Eb2 medial end; muscle strands continuous posteriorly with M. Pb4-Eb2.

RecD3 absent.

Remarks. Muscle reported to be present by Nelson (1969b:18), but he may have considered it the same as the muscle we designate M.Pb4-Eb2 (q.v.). We use RecD to indicate a muscle that connects two successive epibranchials.

RecD4 on posterior edge of cartilaginous tip of Eb3 uncinuate process, fusing posteriorly with posterior end of OD4. Possibly absent, see remarks under OD4.

M. Pb4-Eb2 on Pb4 dorsally and posteromedial cartilaginous edge of Eb2, muscle strands continuous anteriorly with RecD2 (see also remarks under LI3).

Ad1–3 absent.

Ad4 broadly on broad posterolateral surface of

Eb4 and narrowly on dorsodistal surface of Cb4 medial to Eb4-Cb4 joint (not visible in illustrations).

Ad5 slender, from outer edge of dorsoposterior-most distal cartilaginous tip of Eb4 to posterior surface of cartilaginous distal end of Cb5.

Remarks. Winterbottom (1974b:254–255) discussed the problem of what to call a muscle attaching Eb4 to Cb5 when there is only one such muscle. Both OP and Ad5 may exhibit these attachments (Ad5 may attach Cb5 to Eb4, Eb4*, Eb5, or Cb4, but almost always attaches to Eb5 when Eb5 is present (or to Eb4* when this state replaces an autogenous Eb5), exceptions: cyprinids and *Searsia*, Argentiniformes). OP is usually attached well medial to the distal end of Eb4, whereas Ad5 attaches to the distal end (especially when Eb4* is present). Winterbottom recommends using Ad5 for the single muscle, and we concur in the present case, especially as the appearance of the single muscle is more like an Ad5 than an OP, and OP appears to be present in most other osteoglossomorphs (see *Hiodon alosoides*).

RD absent.

SO longitudinal muscle fibers questionably absent, sparse if present.

Additional remarks. SCL absent. TV4 free. Small AC attached to dorsolateral tip of Cb5 (not reported by Nelson, 1968a), found otherwise only in *Pantodon*, thus providing evidence supporting the clade comprising these two genera and *Heterotis*, which lacks the AC. *Arapaima* and *Heterotis* are the only osteoglossiforms we examined that have a glottis (opens dorsally into an air sac), at least one that is so close to the dorsal gill arches. The air sac is joined broadly to the SO, but was not illustrated.

PANTODONTIDAE

Pantodon buchholzi + Peters, USNM 303224 (ca. 80 mm), USNM 353993 (2:50.4–59.2 mm), USNM 355626 (72 mm).

Plate 13

Description (composite).

LE1 absent.

LE2 on dorsoposterior edge of Eb2 somewhat lateral to medial end, meets attachment of TEb1-Eb2 on Eb2.

LE3 absent.

LE4 on dorsoposterior edge of Eb4 somewhat medial to lateral end, meets attachment of OD3–4 on Eb4.

LP absent.

LI1 primarily dorsally on Pb2, wrapping around cartilaginous medial end of Eb1 with slight insertion on medialmost end of Eb1.

LI2 on dorsolateral bony surface of Pb3, insertion posteriorly continuous with that of LI3 Eb4.

LI3 anteriorly on posterolateral cartilaginous end

of Pb3, but mainly on dorsolateral surface of UP5 (few fibers on cartilaginous anteromedial end of Eb4 in one specimen), insertion anteriorly continuous with that of LI2, posteriorly continuous with small group of SO muscle fibers.

TD comprises TEb1-Eb2 and TPb3-Eb4. TEb1-Eb2 divides briefly laterally with short branch attaching to posterior edge of medial end of Eb1, and long branch attaching along posterior edge of medial half of Eb2; continuous posteriorly by few crossing diagonal muscle strands with TPb3-Eb4. TPb3-Eb4 attaches to medial edges and surfaces of Pb3 and Eb4 and is continuous posteriorly (undifferentiated) with SO.

M. Pb2-Eb2 originates on ventroanterior surface of Pb2 (few weak muscle strands may attach on ventromedial end of Eb1) and flares posteriorly as it inserts along dorsoanterior edge of medial half of Eb2.

OD3-4 origin on Pb3 dorsal surface, divides posteriorly with slender branch inserting on Eb3 midposterolaterally and much broader branch inserting on Eb4 mid-dorsolaterally together with insertion of RecD4.

Remarks. Muscle is similar to that of *Notopterus*, q.v.

RecD4 originates ventrally on posteromedial edge of Eb3 and inserts dorsally on Eb4 together with Eb4 branch of OD3-4.

OP questionably absent; however, possibly represented by a thin, narrow band of muscle originating on Eb4 near medial end of Ad4 and scarcely separable medially from OP, fans out ventrolaterally, passing anterior to Ad5, Eb5, and AC, and attaches to Cb5 at and anterior to ventral attachment of Ad5.

ER absent.

Ad1-3 absent.

Ad4 dorsally on posterolateral surface of Eb4, ventrally on Cb4 dorsal surface at anterior angle formed by Eb4-Cb4 joint.

Ad5 dorsally on posterolateral surface of Eb5, ventrally on posterolateral surface of Cb5 together with lateral attachment of TV5.

SO longitudinal muscle fibers questionably present.

SOD broad.

RDs separate, on posterior ends of Pb3 and UP5, which is ventral to Pb3 posteriorly and Eb4 anteriorly.

Remarks. RD is autapomorphic in *Pantodon*.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 and Pb4 absent (we presume that UP4 is also absent and that the large toothplate ventral to Pb3 and Eb4 is UP5). Eb5 and accessory cartilage (AC) present: Eb5 transverse, joined laterally and more-or-less equally to posterodistal ends of Eb4 and Cb4 and medially to dorsal end of AC; AC joined ventrally to dorsodistal end of Cb5. The orientation

of Eb5 is duplicated only in *Diplomystes*, *Ostariophysi*, which lacks AC. Among osteoglossomorphs, AC is found otherwise only in *Arapaima*, thus supporting the clade comprising these two genera and *Heterotis*, which lacks AC.

OSTEOGLOSSIDAE

Osteoglossum bicirrhosum Cuvier, USNM 315447, 210 mm; USNM 198123, 59.6 mm.

Plate 14

Additional material. ② = *Scleropages jardini* (Saville-Kent), USNM 217049, 215 mm.

Description.

Remarks. Because of muscle fusions, our interpretations of LE1, LE2, RecD2, RecD4, and some other problematic muscles of *Osteoglossum* are, in part, subjective, and are described together. The smaller specimen appeared to differ in no significant way from the larger specimen.

LE1 is a thick ribbon of muscle originating on cranium inseparably from dorsal end of Pb1, and inserting along most of the dorsal surface of elongate, cartilaginous Pb1 and dorsomedial end of Eb1. Dorsomedial portion of LE1 insertion on Eb1 joining raphe with anterior end of RecD2, which originates on Eb2 dorsomedially. RecD2 broadens considerably medially, forming what we consider a separate muscle, M. Pb2-Eb2, and attaching anteriorly to dorsal surface of broad cartilaginous anterior end of Pb2 just ventral to insertion of LI1 (anterior end of Pb2 spatulate, becoming almost vertical medial to attachment of M. Pb2-Eb2). At attachment on Eb2, RecD2 joins complex raphe with LE2 insertion, LI3 ventrolateral surface, and anterior end of M. Pb4-Eb2 (described below following OD4). LE2 and LI3 weakly (thinly) continuous dorsal to raphe on Eb2, with LI3 continuing posteroventrally to its insertion. Anterior portion of LI3 insertion on Pb3 just lateral and parallel to LI2 insertion; posterior portion of insertion on cartilaginous Pb4, fusing and attaching inextricably with origin of M. Pb4-Eb2. Anterior end of RecD4 and posterior end of OD3 meet in raphe and attach on medial surface of cartilaginous tip of Eb3 uncinat process. RecD4 attaches posteriorly to mid-dorsal cartilaginous edge of Eb4 anterior to insertion of LE4.

② Anterodorsal portion of LE1 extends dorsal to dorsal end of Pb1 and originates separately on cranium. RecD2 not expanded medially—M. Pb2-Eb2 absent—not attaching to Pb2. LE2 overlaps LI3 laterally, but both muscles are clearly separate anterior to their attachments to Eb2. RecD4 absent.

LE3 on cartilaginous dorsal tip of Eb3 uncinat process.

LE4 broadly along dorsodistal cartilaginous surface of Eb4.

LP absent.

LI1 on lateral surface of vertical expansion (Nelson, 1968a:266) of cartilaginous anterior end of Pb2.

② LI1 in deep excavation on lateral surface of vertical expansion of Pb2.

LI2 on dorsal bony surface of Pb3; medially, insertion parallels and is inseparable from lateral attachment of TD; laterally, LI2 insertion parallels and is medial to anterior portion of LI3 insertion (the two muscles are thin and "plastered" together); posteriorly, insertion impinges on anterior attachment of OD3, which is on posterior cartilaginous end of Pb3.

② Insertion does not impinge on OD3 anteriorly.

LI3 (see initial paragraph under Description above).

TD comprises two portions: short TEb2 and long TPb3-Pb4-Eb4 that is posteriorly scarcely separable from SO. TEb2 is broad, somewhat triangular, with partial median raphe extending posteriorly from muscle's anterior apex; muscle attaches to dorsomedial cartilaginous end of Eb2, where it is inextricably meshed with complex attachments of LE2, LI3, RecD2, and M. Pb4-Eb2. TEb2 is dorsal to and discontinuous from remainder of TD. ② An apparently anomalous strand of muscle is continuous from posterior margin of right side of TEb2 and posteromedial side of OD3.

OD3 on dorsoanterior cartilaginous surface of Pb3 (excluding small, separate anterior cartilaginous segment of Pb3; see Additional remarks, below) and inserts on raphe with RecD4 on medial side of dorsal end of Eb3 uncinat process.

OD4 anteriorly ventral to OD3, originates on anteriormost bony surface of Pb3 medial to LI2 insertion, and inserts on dorsomedial cartilaginous surface of Eb4 just anteroventral to attachment of RecD4.

M. Pb4-Eb2 on Pb4 dorsolaterally, extending anterolaterally and inserting on dorsomedialmost cartilaginous edge of Eb2.

OP probably represented by strap of muscle attaching dorsally to posterior ventromedial surface of Eb4 ventral to Eb4 portion of TD, extending ventrally to ER at about level of mid-distal end of Eb4. ② ER particularly well developed.

Ad1-3 absent.

Ad4 broadly on posterior surface of cartilaginous distal end of Eb4, ventrally, narrowly on dorsodistal bony surface of Cb4.

Ad5 barely separable from SO medially, on posterodistal cartilaginous edge of Eb4 and posterodistal surface of Cb5.

RD absent.

SO longitudinal muscle fibers in thin layer surrounding esophagus. ② Longitudinal fibers in thick

layer dorsally and ventrally, thinner to almost interrupted mid-laterally.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb3 with small, autogenous anterior segment; segment absent in *Scleropages*. Nelson (1968a:268) believed Pb3 cartilage segment among Teleostei to be restricted to *Arapaima* and *Heterotis*, in both of which it is relatively large. He considered its presence an indication that the two genera are closely related. The absence of the segment in *Scleropages* and in some Osteoglossiformes with reduced gill-arch skeletons (e.g., *Pantodon*, *Gymnarchus*), might be secondary.

Elopomorpha: Elopiformes

MEGALOPIDAE

Megalops cyprinoides (Broussonet), USNM 350458, 133 mm.

Plate 15

Additional material. ② = *Megalops atlanticus* Valenciennes, USNM 303317, 146 mm.

Description.

Remarks. Holstvoogd (1965: especially figs. 3a and 3b) illustrated and briefly discussed the dorsal gill-arch muscles of *M. cyprinoides*. Although our findings generally agree with his, we find his illustrations difficult to interpret, and he indicated the presence of only two obliqui dorsales, apparently missing the muscle we identify as OD4.

LE1 on Eb1 just lateral to cartilaginous tip of uncinat process.

LE2 on dorsoposterior edge of Eb2 just anterolateral to SPb2 and medial end of Eb2.

LE3 on Eb3 uncinat process, which articulates with Eb4 uncinat process.

LE4 on dorsodistalmost end of Eb4.

LP absent.

LI1 on Pb2 anterodorsally and on SPb1 anterior surface.

LI2 absent.

LI3 on Pb4 dorsolaterally.

TD comprises TPb3a and TPb3p-Pb4-Eb4. TPb3a is on Pb3 at and anterior to uncinat process; muscle narrows anteriorly and joins CT between anterior ends of Pb3s; posteriorly, TPb3a overlies anteriormost end of TPb3p-Pb4-Eb4 and is continuous with that muscle by slender muscle strand. ② TPb3a entirely anterior to TPb3p-Pb4-Eb4, continuous posteriorly with remainder of TD by broad muscle strand.

OD3 originates on Pb3 ventral to TPb3, partially divided longitudinally, inserts on Eb3 uncinat process.

OD4 originates on Pb3 with and ventral to OD3, and inserts by long tendon anteriorly on Eb4 uncinat process lateral to OD4' insertion.

OD4' originates on Pb3 dorsoposteriorly and on Pb4 dorsoanteriorly and inserts on Eb4 uncinate process medial to OD4 insertion.

OP attaches dorsally on Eb4 posteromedial surface and joins ER ventrally, undifferentiated from SO ventral to ER.

M. UP4-Eb5-Cb4 (not illustrated) questionably distinct muscle strap anterior to (overlain posteriorly by) OP, with dorsoanterior fibers attaching to lateral edge of UP4 and posteroventrally tendinously attaching to junction of Eb5 and Cb4. The alternative to considering M. UP4-Eb5-Cb4 as a distinct muscle is that it is a slightly differentiated SO portion.

Ad1–3 absent.

Ad 4 broadly dorsally on posterodistal margin of Eb4, ventrally on Cb4 posteromedially (not visible in lateral view) medial to internal angle formed by Eb4-Cb4 joint.

Ad5 complex; mainly attaching dorsally to Eb5 posterior surface, but tendinously bound also to posterior end of Cb4; muscle fibers shift directions (featherlike) along mid-axis as muscle extends ventrally, with lateral fibers attaching to Cb5 medially and continuing anteriorly along most of ventral length of Cb5, then changing to broad membranous sheath medial to PCI and PCE (PCI not visible in lateral view, Plate 15C); medial fibers join raphe with TV5.

RD absent.

SO longitudinal muscle layer restricted to isolated area delimited posteriorly by horizontal between distal ends of Eb4s and anteriorly by horizontal between mid-lengths of Pb4s.

Additional remarks. SCL questionable, similar to that of *Elops* (see Additional remarks under *Elops saurus* for discussion of SCL). TV4 free from Cb5s.

Large, tough CT pad covers dorsoanterior surfaces of Pb1s and Pb2s. Eb5 attaches to posterodistal end of Cb4. Johnson and Patterson (1996:273) reported the presence of a small interarcual cartilage between the uncinate processes of Eb3 and Eb4, in *Megalops* and *Elops*. We did not find this cartilage in either specimen of the two *Megalops* species we examined, nor in one cleared and double stained specimen each of *Megalops cyprinoides* (USNM 173580) and *M. atlanticus* (USNM 357435), but we reconfirmed its presence in Johnson and Patterson's specimen of *M. atlanticus* (their specimen of *M. cyprinoides* was unavailable). The presence of the structure is variable and probably of little use for establishing familial interrelationships. In *Elops* (q.v.), the putative rod-like interarcual cartilage is not autogenous, but is an extension of the medial cartilage tip of Eb4. We did find a small cartilage between the tips of the uncinate processes of Eb3 and Eb4 of the albulid *Pterothrissus* (Plate 18), but not in *Albula*, its sister group.

ELOPIDAE

Elops saurus Linnaeus, USNM 121694, 126 mm.

Plate 16

Description.

LE1 on Eb1 near dorsomedial end and ventral to articulation with SPb1.

LE2 on dorsomedial end of Eb2 and entire anterior surface of SPb2; LI2 and LI3 meet LE2 on SPb2.

LE3 on dorsal tip of Eb3 uncinate process, joined there by OD3 insertion.

LE4 attaches by long tendon to dorsodistalmost end of Eb4.

LP absent.

LI1 on Pb2 dorsoanteriorly, attaching to entire medial surface of SPb2; muscle looping anteromedially from posterior attachment to SPb1, forming two sheet-like layers with less extensive posterior layer incompletely overlapping surface of more extensive anterior layer.

Remarks. Unlike *Megalops*, there appears to be no separate origin of LI1 on the braincase, its origin being confined to SPb1.

LI2 on Pb3 posterolaterally and SPb2 medial surface dorsally.

LI3 on lateral edge of Pb4 at junction with UP4, anterior edge attached to SPb2.

TD comprises TPb3 and TPb4-Eb4. TPb3 has two sections: smaller dorsoanterior section dorsally on Pb3 dorsolateral process, overlies anterior end of OD3; larger posterior section on Pb3 lateral edge, attaching posterolaterally along common line with LI2, overlies anterior end of OD4, and is posteriorly continuous by slender, diagonal muscle strand with SO.

Remarks. Winterbottom (1974b:256 and fig. 18) stated that TD is absent in *Elops* because the transverse muscles are continuous with SO. We do not accept that continuation with SO is sufficient basis for rejecting the presence of a transversus muscle. Even if one rejects our TPb4-Eb4 as a transversus, TD is clearly indicated by TPb3 in *Elops*.

OD3 anteriorly on posterior edge of Pb3 dorsolateral process ventral to TPb3 anterolateral attachment; posteriorly on dorsal tip of Eb3 uncinate process together with LE3.

OD4 anteriorly on posteromedial surface of Pb3 and anteromedial surface of Pb4, posteriorly on anterolateral surface of Eb4.

OP dorsally on Eb4 posteriorly, ventromedially joins ER.

Ad1–3 absent.

Ad4 dorsally broadly on posteriormost surface of Eb4, ventrally on posteriormost end of Cb4 lateral to Eb5 ventrally.

Ad5 dorsally on medial junction of Cb4 and Eb5, curving first ventromedially around posterior end of

Cb5, then laterally, attaching along lateral surface of Cb5.

RDs absent.

SO longitudinal muscle layer restricted to isolated area delimited posteriorly by horizontal between distal ends of Eb4s and anteriorly by horizontal at anterior end of TPb4-Eb4.

Additional remarks. TV4 free from Cb5s. Presence of SCL questionable: Hb3 posteroventral flange is straight anteriorly, curves medially posteriorly, and is attached tightly to posteroventral cartilaginous process of Bb3, thus forming with contralateral Hb3 an anteriorly open semicircle, the edge of which is lined with CT. ObV3, on each side, attaches along the lateral edge of the straight portion of the Hb3 flange and is muscously continuous medially with its respective RecV4, which attaches to the posterior edge of the curved portion of the flange, but not to the cartilaginous tip of Bb3. There is no free ligamentous portion along the semicircle, but if some portion were free, we would interpret the semicircular ligament as being present. (*NB.* There is no autogenous ball of cartilage ventral to the posteroventral tip of Bb3, as is present in *Albula*.) *Megalops* (both species) is similar to *Elops*, but Hb3s do not curve medially posteriorly, the CT lining the semicircle is slightly loose, and RecV4 is attached to the posterior margin of the posteroventral cartilaginous process of Bb3.

Nelson (1968b:fig. 6a) indicated the presence of an interarcual cartilage between the uncinat process of Eb3 and the proximal end of Eb4. Johnson and Patterson (1996:273) claimed to have confirmed this. Our observations differ. The "interarcual cartilage" of our specimen, and Johnson and Patterson's, on re-examination, is a non-autogenous, elongate cartilaginous extension of the dorsomedial cartilaginous head of Eb4. The extension attaches to the tip of the Eb3 uncinat process. Conceivably, this cartilaginous extension could bud off in large specimens, and such should be examined to determine if this occurs. See also Additional remarks under Megalopidae.

Elopomorpha: Anguillomorpha

ALBULIDAE

Albula vulpes (Linnaeus)?, USNM 247511, 127 mm SL.

Plate 17

Description.

LE1 broadly on Eb1, attaches to skull separately from other LEs, incorporates tendon dorsally.

LE2 broadly on Eb2, incorporates tendon dorsally.

LE3 on Eb3 uncinat process ventral to cartilaginous tip.

LE4 on anterior surface of levator process of Eb4 just ventral to cartilaginous edge.

LP absent.

LI1 on Pb2 anteriorly, comprises two ventrally continuous sections; anterior section shorter than posterior section, attached all along medial surface of cartilaginous SPb1.

Remarks. See remarks under LI1 in *Aldrovandia* (Halosauridae) description.

LI2 on dorsolateral bony portion of Pb3.

LI3 on dorsolateral edges of UP4 and UP5, insertion continuous medially with attachment of M. UP4-Eb2.

TD comprises two, more-or-less continuous sections, TPb3a, which attaches along anterior margin of Pb3 dorsal process, and TPb3p-UP4, which attaches laterally to medial edges of Pb3 and UP4, abutting OD4 ventromedial margin; separable posterolaterally from SO by slight change in orientation of muscle fibers, but continuous posteriorly otherwise with SO.

OD3 long, slender, originates on bony portion of Pb3 dorsal process and inserts on cartilaginous tip of Eb3 uncinat process; anomalous slip of muscle arises from origin of left-side OD3, passes through TPb3 and inserts on cartilaginous tip of Eb3 uncinat process.

OD4 large, vertically oriented; ventromedially abutting TPb3; origin curving medially, attaching continuously from posterodorsal edge of Pb3, across medial cartilaginous process of Eb3, over Pb4 to base of Eb4; muscle twisting on itself dorsally (clockwise on right side, counterclockwise on left), almost divisible into two parts, inserting on dorsomedial (uncinat) process of Eb4.

Remarks. Wiley (1976:fig. 13c) believed this muscle to be a transversus dorsalis posterior and made no mention of the muscle we treat as TPb3-UP4. Whatever the homology may be, we do not believe our OD4 is a homologue of a transversus dorsalis, which we consider to be a muscle joining the two sides of the gill arches. A vertically oriented OD4 is known only in albulids.

OP dorsally on posterior surface of Eb4 medial to uncinat process, where it overlaps M. UP5-Cb4, ventrolaterally joining ER, below which Ad5 and SO appear to be confluent.

OP' slender, originating on dorsoposterior bony surface of Eb4 uncinat process (attachment covered by OD4) and inserting tendinously at ER.

Remarks. Although present on both sides of our specimen, verification in other specimens is needed.

M. UP4-Eb2 origin on UP4 continuous with medial end of insertion of LI3; insertion on cartilaginous cap of Eb2 dorsomedial (uncinat?) process.

Remarks. Similar muscle, M. Pb4-Eb2 present in *Aldrovandia affinis* (Halosauridae).

M. UP5-Cb4 dorsally with some fibers attaching to Eb4, but main portion of muscle continuing anteriorly ventral to Eb4 and attaching to dorsal surface

of UP5; posteroventrally attaching to anterior surface of fingerlike (fused Eb5) posterior cartilaginous end of Cb4.

Remarks. M. UP5-Cb4 is known elsewhere only in *Pterothrissus*.

Ad1–3 absent.

Ad4 large, prominent, on posterior surface of Eb4 levator process and posterior end of Cb4.

Ad5 undifferentiated medially from SO, joined dorsomedially to ER; attaches dorsolaterally to cartilaginous rod-like posterodistal end of Cb4 and ventrally along lateral half of posterior surface of Cb5.

Remarks. *Albula* lacks Eb5; however, the conformation of the cartilaginous distal end of Cb4 appears similar to the combined distal end of Cb4 and Eb5 in *Pterothrissus*, presumably indicating fusion of these two elements in *Albula*. The possibility of such fusion is indicated by our specimen of the anguillomorph *Notacanthus* (Notacanthidae), in which Eb5 is autogenous on one side and, based on appearance, fused with Eb4 on the other.

SO longitudinal layer appears to be restricted, at least dorsally, to isolated area ventral to TPb3 (not present immediately posterior to TPb3).

RD absent.

Additional remarks. SCL attaches mid-dorsally to small, autogenous cartilaginous ball, which attaches in turn to ventral surface of cartilaginous tip of posterior end of Bb3 (anterior end of RecV4 attaches to SCL; ObV3 attaches medially only to Hb3 flange continuous with SCL). A relatively larger, somewhat cone-shaped autogenous cartilage is present in a smaller cleared-and-stained specimen examined (autogenous cartilaginous element attached to ventro-posterior tip of Bb3 is known otherwise only in some acanthomorphs, e.g., the melamphaid *Poromitra capito*, q.v., which lacks SCL). The autogenous cartilage was not mentioned by Nelson (1969a, fig. 7a). TV4 is free from Cb5s, but is attached to ventral surface of Bb4. Pb1 is oriented horizontally—in line with Eb1. SPb2 is absent; cartilaginous SPb1 articulates with medial end of Eb1 (as opposed to ossified SPb1 in *Elops* and *Megalops*, both of which have cartilaginous SPb2s).

Pterothrissus gissu Hilgendorf, FRSKU 22120, 132 mm.

Plate 18

Description.

LE1 on Eb1 mid-dorsoposteriorly and on lateral surface of SPb1 dorsally ventral to origin of muscle.

LE2 on anterior surface of Eb2 uncinat process, originates by long tendon (all other levators originate musculously).

LE3 on anterior surface of Eb3 uncinat process.

LE4 on dorsal cartilaginous tip of Eb4 levator process.

LP absent.

LI1 on dorsal surface of Pb2 and medial surface of SPb1.

Remarks. See remarks under LI1 in *Aldrovandia* (Halosauridae) description.

LI2 on posteromedial surface of Pb3 ventral to OD4.

LI3 on dorsolateral edges of UP4 and UP5.

TD comprises TPb3 and TPb4. TPb3 divided into anterior and posterior sections by OD3, which originates on Pb3 ventral to anterior section; anterior section attaches to anterolateralmost surface of Pb3 uncinat process; posterior section attaches to uncinat process just ventral to anterior section and is continuous posteriorly by diagonal muscle strand with TPb4. TPb4 attaches to dorsomedial cartilaginous edge of Pb4 along line with OD4 origin.

OD3 origin on dorsoanterior bony Pb3 surface below TPb3 anterior section; insertion on dorsoanterior-most edge of tip of Eb3 uncinat process.

OD4 large, vertically oriented; anteromedially, muscle originates continuously along bony dorso-medial margin of Pb3 and medial margin of Pb4 at junction of cartilage and bony UP4; dorsolaterally, muscle divides into two sections: posterior section inserts on Eb4 uncinat process and small AC at tip of process, anterior section extends posteriorly passing ventral to insertion of posterior section and inserts broadly on anterior surface of Eb4 levator process.

Remarks. A vertically oriented OD4 is known only in albulids.

OP dorsally on posteromedial surface of Eb4, ventrally ending at ER.

M. UP5-Cb4 dorsally with some fibers attaching to Eb4, but main portion of muscle continuing anteriorly ventral to Eb4 and attaching to dorsal surface of UP5; ventrally attaching broadly to posterodistal end of Cb4 with minor attachment to Eb5 medial surface.

Remarks. M. UP5-Cb4 is known elsewhere only in *Albula*.

Ad1–3 absent.

Ad4 large, prominent, dorsally on posterior surface of Eb4 levator process, ventrally on Cb4 dorsoposterior surface anterior to inner angle formed by Eb4-Cb4 joint.

Ad5 on Cb4 posterodistal end, wraps medially around distal end of Cb5 and attaches to Cb5 posteroventral surface beginning at about mid-length, joined dorsomedially to ER and ventromedially by raphe with TV5.

SO longitudinal muscle layer attaches anteriorly to Pb3.

RD absent.

Additional remarks. SCL attached mid-dorsally to posteroventral cartilaginous tip of Bb3. TV4 free from Cb5s, but mid-dorsal surface attaches to Bb4 ventral surface. Small, autogenous ball of cartilage (AC) present between dorsalmost cartilaginous tips of Eb3 and Eb4 uncinat processes. Another AC at inner angle formed by Eb1-Cb1 joints, supports gill raker at joint. Large, more-or-less vertically oriented Eb5 attaches to posteromedialmost tip of Cb4. Eb5 appears to be represented by non-autogenous process at posteromedialmost end of Cb4 in *Albula*. Pb1 cartilaginous (ossified in *Albula*).

NOTACANTHIDAE

Notacanthus chemnitzii Bloch, USNM 214342, ca. 340 mm.

Plate 19

Description.

LE1 on mid-posterior edge of Eb1 just lateral to uncinat process.

Remarks. Slender ligament, originating on skull, inserts on medial end of Eb1; similar ligament inserts on medial end of Pb2 in related *Aldrovandia* (Halo-sauridae).

LE2 on Eb2 uncinat process.

LE3 on cartilaginous tip of Eb3 uncinat process; muscle present and well developed only on left side of illustrated specimen (but presence indicated in illustration based on USNM 44246, examined in situ, in which LE3 is present on both sides).

LE 4 absent (both specimens).

LP absent.

LI1 on dorsal surface of Pb2.

LI2 on dorsal surface of posterolateral cartilaginous process of Pb3.

LI3 absent (Pb4 absent).

TD comprises three continuous portions that are demarcated only laterally: TEb2, TPb3, and TEb4. TEb2 attaches to anterior surface of medialmost end of Eb2, dividing laterally as it passes over anterolateral cartilaginous process of Pb3, to which a few strands of muscle also attach; TPb3 attaches to dorsolateral surface of Pb3; TEb4 attaches to posteromedial edge of Eb4 and is broadly continuous posteriorly with SO.

OD3 absent.

OD4 with split origin: on Pb3 dorsally ventral to TEb2, and on tip of Eb2 uncinat process; origins fuse posteriorly and insert on Eb4 dorsodistally.

Remarks. Origin on Eb2 is unique.

OP distinct, ribbon-like, originating dorsally on posteromedial surface of Eb4 and extending posteroventrally, then curving anteriorly and joining contralateral OP in medial raphe, anterior point of which joins medial raphe of TV5. As such, OP does

not attach ventrally to a gill-arch element. ER is absent.

Ad1–3 present. Ad1 relatively large, inseparable from gill-filament muscle, which appears to overlie it dorsolaterally, but is continuous with it ventromedially. Ad2 and 3 well developed, with well-developed gill-filament muscle portions dorsoanteriorly. Lateral portions of gill-filament muscles of Ad2 and 3 were destroyed during dissection and their full extent is unknown (see also remarks under Ad1–3 in *Oncorhynchus* (Salmoniformes)).

Ad4 relatively large, dorsally on long dorsoposterior edge of Eb4, ventrally on much of posterodorsal surface of Cb4.

Ad4', small (smaller than Ad3), vertical muscle band, dorsally on anterodistal surface of Eb4, ventrally on bony anterolateral surface of Cb4; apparently not associated with gill-filament muscle.

Remarks. Ad4' appears to be an autapomorphy and was not observed elsewhere in this study. It differs from Ad4 in attaching to the anterior surface of Cb4, whereas Ad4 in pre-acanthomorphs, except *Polyodon*, attaches to the dorsoposterior surface of Cb4 just medial to internal angle formed by Eb4-Cb4 joint. In *Polyodon*, Ad4 attaches to posterior surface of Eb4 and anterior surface of Cb4.

Ad5 enveloped in tough CT (removed in Plate 19); on left side attaches dorsally to Eb5, which is attached to distalmost surfaces of Eb4 and Cb4; on right side attaches dorsally to cartilaginous Eb4 process that has shape and position of separate Eb5 on left side; relatively long and free as it wraps around Cb5 and attaches well medially on Cb5.

Remarks. In a cleared and stained specimen (USNM 214339), Eb5 is present on both sides and it is equally associated with the cartilaginous ends of Eb4 and Cb4. Cb5 bears simple gill rakers but no teeth.

RD absent.

SO longitudinal muscle layer present (not illustrated), spongy, extends anteriorly beyond horizontal between medial ends of Eb1s.

Additional remarks. SCL absent. TV4 free from Cb5s, but attached to mid-anteroventral surface of Bb4. Pbl absent, apparently replaced functionally by elongate cartilaginous end of Eb1. Pharyngobranchial toothplates absent. Bb1 bears edentulous tooth plate mid-dorsally, not reported by McDowell (1973:132) in *Notacanthus*. Tough, slender ligament on anterolateralmost edge of anterior cartilaginous end of Eb1 (originates on ventral margin of opercular bone McDowell, 1973:132). Slender ligament (not illustrated) originates on skull separately from clustered origins of LEs and LIs and inserts on Pb3 medial to Pb3 origin of OD4.

HALOSAURIDAE

Aldrovandia affinis (Günther), USNM 319707, ca. 425 mm TL.

Plate 20

Description.

LE1 on base of Eb1 uncinat process.

LE 2 on anterior surface of Eb2 uncinat process along and ventral to posterior cartilaginous tip of process, which also has separate cartilaginous dorsoanterior tip (see M. Pb4-Eb2).

LE3 on cartilaginous tip of Eb3 uncinat process at attachment of Eb3 branch of OD3–4.

LE4 on cartilaginous tip of Eb4 levator process.

Remarks. Slender ligament, originating on skull, also inserts on levator process. Similar ligament also present in closely related *Notacanthus* (Notacanthidae), which lacks LE4.

LP absent.

LI1 inserts over most of dorsoanterior surface of Pb2 and on cartilaginous tip of Eb1 uncinat process.

Remarks. Long, ribbon-like ligament, originating on skull, inserts on medial tip of Pb2. Similar ligament, inserting, however, on medial end of Eb1, present in related *Notacanthus* (Notacanthidae).

The unusual partial insertion of LI1 to include the medial end of Eb1 may be the result of the loss of SPb1. In some other elopomorphs (*Elops*, *Megalops*, *Albula*, and *Pterothrissus*), SPb1 is present and attaches on the dorsomedial end of Eb1 (which presumably divides to become the uncinat process), and LI1 expands ventrally to almost completely envelop SPb1 in its insertion, which is otherwise on Pb2. The insertion on SPb1 just misses including the edge of Eb1, so that it would be no great change for LI1 to have its insertion extended (as in *Aldrovandia*) to include the tip of the uncinat process if SPb1 were lost. Compare LI1 in *Aldrovandia* with LI1 in *Elops*, *Megalops*, *Albula*, and *Pterothrissus*.

LI2 on dorsolateral edge of Pb3.

LI3 broad based, anteriorly on cartilaginous Pb4 at junction of cartilage with UP4, continuing posteriorly onto edge of UP5, the anterior edge of which lies under posterior end of Pb4.

M. Pb4-UP5-Eb2 origin on posterolateral corner of Pb4 continuous anteriorly with insertion of LI3, posteriorly on dorsolateral surface of UP5 (not illustrated); insertion on osseous dorsal edge of Eb2 uncinat process.

TD comprising continuous TPb3-Pb4-Eb4 with additional, roughly trapezoidal TPb3 section arising mid-dorsally from TPb4 area; anterior fibers of separate section, attaching to and wrapping anteriorly around cartilage-tipped lateral process of Pb3; TD completely undifferentiated posteriorly from SO.

OD3–4 origin broadly continuous on posterior edge of Pb3 and anterior end of Pb4, dividing pos-

teriorly with one section inserting on Eb3 uncinat process and other section inserting on Eb4 anterolaterally.

OP dorsally on ventral surface and posteromedial edge of Eb4; ventrally on small Eb5 attached to Cb4 and dorsodistal cartilaginous end of Cb4. ER absent.

Ad1–3 absent.

Ad4 on Eb4 dorsoposteriorly and dorsoposterior bony surface of Cb4.

Ad5 dorsally on Cb4 distally and tiny Eb5, which articulates ventrally with Cb4 and is attached by ligament to Eb4 levator process; free ventrally for short distance posterior to attachment on mid-ventromedial surface of Cb5.

RD absent.

SO longitudinal muscle layer (not illustrated) extends anteriorly at least to horizontal between medial ends of Eb1s. SO fibers also attach to UP5, which is ventral to, but separated by SO and OP muscle fibers from medial arm of Eb4.

Additional remarks. SCL absent. TV4 free from Cb5s. Ligament connects posterior bony surface of Eb2 uncinat process to anterodistal cartilaginous end of Eb3; another connects posterior bony surface of Eb3 uncinat process to anterodistal cartilaginous end of Eb4; another attaches tip of Eb4 uncinat process to Eb5, which, unusually, attaches to Cb4 rather than Eb4, and continues dorsoposteriorly. Ribbon-like ligament inserts on cartilaginous tip of medial process of Pb2; its origin was not recorded, but a similar ligament in *Notacanthus* attaches to the cranium. Pb2 lacks tooth plate.

CONGRIDAE

Conger cinereus Rüppell, USNM 115969, 345 mm.

Plate 21

Description.

Remarks. Nelson (1967c) described and illustrated the gill-arch musculature of *Conger marginatus* (currently considered a junior synonym of *C. cinereus*). Insofar as Nelson's and our findings can be compared, there is much similarity, but some differences mentioned below suggest further study is indicated. Although there is a question about the homology of the pharyngeal tooth plates, we use Nelson's (1966b) terminology for convenience.

LE1 tendinously on Eb1 mid-dorsoposteriorly.

LE2 tendinously on Eb2 mid-dorsoposteriorly.

LE3 on cartilaginous tips of joined Eb3 and Eb4 uncinat processes.

LE4 finely, tendinously on Eb4 mid-dorsally.

LP absent.

LI1 on cartilaginous medial end of Pb2.

LI2 on Pb3 laterally, UP3 dorsolaterally, and UP4 dorsoanterolaterally.

LI3 absent (Pb4 absent).

TD thin, sheet-like, overlies SO posteriorly, but scarcely separable from SO, comprises TPb3-Eb4, attaching dorsally on Pb3 at and along line of attachment of OD4, and on Eb4 anteromedially.

OD3 absent.

OD4 origin on Pb3 medial to LI2 and lateral to line of attachment of TPb3-Eb4, insertion along entire length of Eb4 uncinat process.

Remarks. The tips of the uncinat processes of Eb3 and Eb4 are tightly bound together, and OD4 is possibly minutely attached to the cartilaginous tip of Eb3 uncinat process. In contrast to our findings, Nelson (1967c:349) reported that the superior oblique (= our OD) in *C. marginata* attaches Pb3 only to Eb3. If it is determined that the OD of *C. cinereus* lacks a "true" connection to Eb3, the lack is autapomorphic. An OD attachment to Eb3 defines the Teleostei, and there are exceedingly few other pre-acanthomorph taxa that lack the attachment (i.e., *Notacanthus*, *Gonostoma*, *Maurolicus*).

RecD2 on ventroanteriormost surface of Eb2 and mid-posterior edge of Eb1.

RecD3 on ventroanteriormost surface of Eb3 and mid-posterior edge of Eb2.

M. Pb2-Eb1 on Pb2 dorsoposteriorly and Eb1 medial cartilaginous tip.

Remarks. Nelson (1967c:349 and fig. 2) termed this muscle obliquus inferior accessorius.

M. UP4-Eb4 on UP4 dorsoposterolaterally, posteriorly becoming broad, thin CT sheet, which attaches to ventrolateral margin of Eb4 (at angle of Eb4-Cb4 joint) and extends medially, becoming incorporated in SO.

Remarks. Nelson (1967c:349) termed this muscle "retractor dorsalis." Although appropriately named functionally, the muscle does not originate on the vertebral column and cannot be considered even homoplastically as RD. Nelson (1966a:123), however, reported that [exceptionally] among the several eels he examined, which also included *Conger* and *Anguilla*, but not *Synphobranchus*, "RD" in the [specialized] Muraeninae, has become attached secondarily to the vertebrae.

OP strap of muscle attaching dorsally to Eb4 posteromedially, slightly distinguished by denser fibers from SO medially, ending ventrally at ER, which is joined ventrally by Ad5; ventromedially partially overlain by SO fibers.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteroventral surface and ventrally on Cb4 posterodorsal surface.

Ad5 joins distal end of Cb5 to bony sub-distal end of Cb4, dorsomedially joining ER.

RD absent. See SO.

SO thin longitudinal muscle layer surrounds esophagus and attaches to toothplates and Pb3.

Additional remarks. SCL absent. TV4 free from Cb5s. Uncinate process present on Eb4. Pb1 absent.

ANGUILLIDAE

Anguilla rostrata (Lesueur), USNM 340815, 228 mm, USNM 190998, 328 mm.

Plate 22

Description.

Remarks. All levators extend lateral to LI1, except LE4, which passes medial to LI1. LI1 extends dorsolaterally, all other levators extend anteriorly. Nelson (1967c) described and illustrated the gill-arch musculature of *Anguilla rostrata*. There is much similarity between his and our findings, but a few differences exist.

Although there is a question about the homology of the pharyngeal tooth plates, we use Nelson's (1966b) terminology for convenience.

LE1 on dorsal surface of Eb1 about half length distally.

LE2 on dorsal surface of Eb2 about half length distally.

LE3 finely tendinously on dorsoanterior surface of bony Eb3 uncinat process, just ventral to OD3 insertion.

LE4 very slender, on Eb4 mid-dorsally just lateral to bony uncinat process, which is tightly joined to bony Eb3 uncinat process.

LP absent.

LI1 broad, thin, on Pb2 dorsal surface; insertion just medial to and paralleling M. Pb2-Eb1.

LI2 on UP3 dorsolaterally.

Remarks. Nelson (1967c:349) did not describe the insertion of LI2 in either *Anguilla* or *Conger*, but reported that the muscles of *Anguilla* are "rather similar" to those of *Conger*. In *Conger*, LI2 inserts on Pb3, UP3, and UP4.

LI3 absent (Pb4 absent).

TD comprises TPb3-UP3-UP4-Eb4, on medial margin of Pb3, just barely on posteromedial edge of UP3, on dorsomedial surface of UP4, continuing uninterrupted posteriorly as SO, and medial tip of Eb4.

OD3 origin on dorsoanterior end of Pb3, continuous with OD4 origin, insertion on bony Eb3 uncinat process dorsal to LE3.

Remarks. Nelson (1967c:fig. 4) indicated that OD4 attaches to a cartilage tipped Eb4 levator process. In both our specimens, the tips of the levator processes on Eb3 and Eb4 are bony and although the two processes are tightly bound together by CT, OD3 attaches only to Eb3.

OD4 origin on Pb3 dorsoposteriorly, insertion on Eb4 anteromedial edge.

RecD1 very long, on Eb1 anterodistal tip, anteriorly ends tendinously in CT of roof of mouth, parallels LEs.

Remarks. Ordinarily we would consider this muscle as LE1', but its serial position, like that of RecD2 and RecD3, supports Nelson's (1967c) assignment (our RecD is the same as Nelson's *obliquus inferior accessorius*). With the questionable exception of the osteoglossiform *Gymnarchus*, we know of no other genus in which RecD1 occurs.

RecD2 short, posteriorly on anterodistal end of Eb2, joined along anterior edge by well-developed portion of GFM, on Eb1 posterolaterally posterior to LE1 insertion.

RecD3, short, on anterodistal end of Eb3, joined along anterior edge by well-developed portion of GFM; on Eb2 posterolaterally posterior to LE2 insertion.

M. Pb2-Eb1 small, hidden by LI1, anteriorly on medial tip of Eb1, posteriorly on lateral edge of Pb2, parallels lateral side of LI1 insertion.

OP dorsally on Eb4 dorsomedially, ventrally joins ER with SO and Ad5, not continuous below ER, which extends tendinously laterally and attaches to Cb4 distally together with dorsal end of Ad5.

Ad1–3 absent.

Ad4 dorsally on posterior edge of Eb4, ventrally on Cb4 anterior to Eb4-Cb4 joint.

Ad5 dorsally on ER with lateral tendinous attachment to Cb4 posterodistal end; ventrally on posterodistal half of Cb5.

RD absent. See SO below.

SO longitudinal muscle layer surrounds esophagous, dorsally fibers attach to tooth plates and medial margin of Pb3.

Remarks. Nelson (1967c) considered this portion of the longitudinal muscle layer as RD.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 absent.

SYNAPHOBRANCHIDAE

Synaphobranchus sp., USNM 316662, ca. 340 mm.

Plate 23

Remarks. Although there is a question about the homology of the pharyngeal tooth plates, we use Nelson's (1966b) terminology for convenience.

Description.

LE1 broadly on Eb1 dorsally beginning at about mid-length of bone and extending laterally to small posterodistal flange-like process.

LE2 on small posterodistal Eb2 flange-like process.

LE3 on posterior flange-like Eb3 process at OD3–4 insertion.

LE4 on Eb4 dorsally slightly distal to mid-length.

LP absent.

LI1 on Pb2 anterolaterally.

LI2 inserts posteriorly on Pb3 dorsoposteriorly,

UP3 dorsomedially, and on anterodorsal edge of UP4, and inserts anteriorly on dorsoposterior edge of Eb2.

LI3 absent (Pb4 absent).

TD comprises undifferentiated layer of muscle, TPb3-UP3-UP4, attaching laterally to Pb3, UP3 dorsomedially, and on most of dorsal surface of UP4.

OD3–4 origin on anterior end of Pb3, insertion on Eb3 dorsally at and posterior to insertion of LE3 and on anteromedial edge of Eb4 beginning well lateral to joint with Pb3 and ending just proximal to point opposite insertion of LE3.

M. Pb2-Eb2 attached to ventral surfaces of Pb2 and anterior end of Eb2.

RecD2 on proximal two-thirds of anterior edge of Eb2 and on dorsomedial tip of Eb1.

OP questionably present as strap of muscle attaching dorsally to posteromedial surface of UP4 and ending ventrally at ER, which is at level of Cb4 and extends laterally as slender tendon to posterodistal end of Cb5; inseparable medially, and ventral to ER, from SO.

Remarks. The shift of the dorsal attachment of OP from Eb4 to UP4 is unique among the taxa we examined. Nelson (1967c) considered this muscle section as RD.

Ad1–3 absent.

Ad4, very large, dorsally on most of Eb4 posterior surface, ventrally on Cb4 dorsal surface anterior to internal angle formed by Eb4-Cb4 joint.

Ad5 absent.

RD absent. See SO.

SO thin, longitudinal muscle layer extending anteriorly to horizontal between anterior tips of Pb3s, surrounding esophagous, attaching to toothplates and Pb3.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb2 reduced, cartilaginous. Pb1 absent.

Clupeomorpha

DENTICIPITIDAE

Denticeps clupeoides Clausen, USNM 358795, 36.4 mm, and BMNH uncataloged, 2 specimens, 30.0–30.6 mm.

Plate 24

Description.

Remarks. All levators except LI1 extend anteriorly, horizontally, at almost 180° angle and form a thin, posteriorly concave fan of overlapping muscles that is closely applied to, and originates on, the convex surface of the otic bulla. LI1 extends laterally at about 90° angle from other levators, is medially concave, and conforms with the laterally convex surface of the otic bulla on which it originates.

LE1 on minute cartilaginous tip of poorly developed Eb1 uncinat process.

LE2 on minute cartilaginous tip of poorly developed Eb2 uncinat process.

LE3 on minute cartilaginous tip of well-developed Eb3 uncinat process.

LE4 on cartilaginous dorsomedial end of Eb4 uncinat process, there meeting OD4 insertion.

LP absent.

Remarks. Greenwood and Lauder (1981:226) were uncertain that LP was absent in *Denticeps* because of the small size (ca. 50 mm SL) of their specimens. We agree that size was a problem for dissection and illustration, but are confident that LP is absent.

LI1 on Pb2 posterolaterally (see also remarks at beginning of description above).

LI2 on Pb3 posterolaterally.

LI3 on cartilaginous Pb4 (not illustrated) posterolaterally.

TD comprises TEb2 and TPb3-Pb4-Eb4. TEb2 attaches to Eb2 dorsomedially. TPb3-Pb4-Eb4 on Pb3 and Pb4 at and along part of OD4 origin, becoming wider posteriorly and attaching on dorsal surface of Eb4 medial to uncinat process.

OD3 origin on Pb3 dorsal surface ventral to TEb2, continuous with OD4 origin, and insertion on Eb3 uncinat process.

OD4 originates on Pb3 dorsoposterior surface ventral to TEb2, and on Pb4 dorsal surface at and medial to Pb4 portion of TPb3-Pb4-Eb4, and inserts on anteromedialmost surface of Eb4 uncinat process.

OP slender strap of muscle, dorsally on posteromedial edge of Eb4 uncinat process, overlapping much of Ad4 posterior surface, ending ventrally at ER, which is dorsal termination of major portion of Ad5 (unless continuation is interpreted as OP fused laterally with AD5).

Ad1-3 absent.

Ad4 dorsally on dorsoposterior edge of Eb4 uncinat process continuing to distal end of Eb4, ventrally on Cb4 dorsal edge anterior to internal angle formed by Eb4-Cb4 joint.

Ad5 dorsally on posterior surface of Eb5 and at ER ventral to OP, medially continuous with SO, ventrally on Cb5 posterior surface.

SO longitudinal muscle layer thickest dorsally and ventrally; anterior extent undetermined.

RDs absent.

Additional remarks. SCL absent. TV4 free from Cb5s. Eb5 present (not previously reported, although possibly implied by discussions in Johnson and Patterson, 1996). A single large UP present.

Description.

LE1 slender, weak, on dorsal bony edge of Eb1 uncinat process just distal to cartilaginous tip.

LE2 slender, weak, on dorsal bony edge of Eb2 uncinat process just distal to cartilaginous tip.

LE3 on tip of all bony Eb3 uncinat process, at and anteromedial to LE3' insertion, larger and angled dorsoanteriorly about 10° lower than LE3'.

LE3' on tip of all bony Eb3 uncinat process at and posterior to LE3 insertion, slenderer and angled dorsoanteriorly about 10° higher than LE3.

LE4 broad, thin, on bony dorsoposterior edge of Eb4* coincident with posterior edge of OD4 insertion; questionably comprising two very thin sections, anterior and posterior, on right side, but not on left side.

LP broad, thin, on dorsodistal cartilaginous edge of Eb4*, commencing at lateralmost edge of LE4 insertion, partially coincident with Ad4 dorsal attachment.

LI1 on Pb2 dorsal surface medial to uncinat process.

LI2 on Pb3 dorsoposteriorly.

LI3 on Pb4 (not illustrated) dorsoposteriorly.

TD comprises TPb3-Pb4-Eb4*, slightly partitioned laterally at posterolateral origin of OD4 on Pb3 and at attachment to medial end of Eb4*; on right side only, joining ER with OP ventrally; continuation posteriorly with SO marked by change in muscle fiber direction.

OD3 origin on Pb3 dorsal surface anterior to uncinat process and on medial edge of uncinat process; insertion on dorsomedial edge of Eb3 bony uncinat process.

OD4 origin begins on Pb3 among TD fibers, passing dorsal to most of Pb3 attachment of TD, and continuing on Pb4 dorsoanteriorly; insertion broadly dorsally on Eb4* anterior surface ventral to LE4 insertion.

OP strap of muscle originating on Eb4* posteromedial to LE4 insertion, and extending ventrally to ER; undifferentiated from SO ventral to ER.

Ad1-3 absent.

Ad4 dorsoposteriorly on Eb4*, ventrally on Cb4 at anterior angle formed by Eb4*-Cb4 joint.

Ad5 dorsally on distal end of Eb4*, ventrally on Cb5 distal end, inseparable mid-medially from SO.

RD absent.

SO longitudinal muscle layer spongy, circumesophageal, thickest dorsally, extending dorsoanteriorly to below anterior end of TD, but becoming extremely attenuated anterior to horizontal between medial ends of Eb4*s.

Additional remarks. SCL absent. TV4 free from Cb5s, attached dorsally to ventral surface of Bb3. Tiny MSPb1 anterior to anterior end of each Eb1. GC attached ventrally to anterior ends of Pb2s, which

PRISTIGASTERIDAE

Ilisha africana (Bloch), USNM 357405, 120 mm.

Plate 25

are slightly dorsal to anterior ends of Pb3s (see also Additional remarks under *Cetengraulis*, and *Chanos*).

ENGRAULIDAE

Cetengraulis edentulus (Cuvier), USNM 186377, 2 specimens, 118–124 mm.

Plates 26.1, 26.2

Description.

Remarks. All levators except LE1 pass medial to LI1. LE2–4 extend horizontally anteriorly at approximately 180° from insertions, LE4' extends dorsoanteriorly about 15° from insertion, LI is more-or-less vertical, and LI2 and LI3 are angled dorsoanteriorly about 45°.

LE1 thin, slender, on bony process at distal edge of base of Eb1 uncinat process; originates somewhat more anteriorly on skull than other LEs.

LE2 on tip of Eb2 uncinat process.

LE3 tendinously on Eb3 uncinat process ventral to OD3 insertion.

LE4 on medial edge of Eb4* levator process dorsal to insertion of OD4; originates as long tendon.

LP slender, membranously attached along lateral edge of LE4, inserting with LE4 insertion; originates as very long, slender tendon.

LI1 broad, thin, convex medially (medial surface conforming with surface of cranium), inserting broadly on dorsal surface of Pb2.

LI2 on posterior end of Pb3 dorsal surface.

LI3 inserting as long, slender tendon on medial edge of Pb4 dorsoanteriorly.

TD comprises TPb3, TPb4, and TEb4*. TPb3 separate muscle attaching to dorsolateral edge of Pb3 beginning just posterior to base of uncinat process, continuous posteriorly by diagonal strand of muscle inserting on Pb4 anteriorly in one specimen and at mid-length on other. Anteriorly, TPb4 comprises loose strands of fibers, which attach on each Pb4 dorsomedially, and is continuous posteriorly with slender TEb4*, which attaches to ventromedial ends of Eb4*s and is continuous posteriorly with SO+EO.

OD3 slender, originates on Pb3 uncinat process ventromedial to dorsal tip and inserts tendinously on Eb3 uncinat process just ventral to tip and dorsal to LE3.

OD4 very weak, almost thread-like, originates by short, fine tendon attached to tiny (almost pinpoint) bony area on dorsomedial edge of otherwise cartilaginous Pb4; inserts on ventromedial edge of Eb4*.

OP unclear if absent or included in complex surface muscles on EO.

Ad1–3 absent.

Ad4 two widely separated dorsal attachments posteriorly on Eb4* levator process, uniting ventrally in slender attachment (not visible in lateral view) on Cb4 at innermost angle formed by Eb4*-Cb4 joint.

Ad5 questionably included in complex surface muscles arising from EO and Cb5 and attaching anterolaterally to Eb4*.

Remarks. There is a posteroventral, rod-like cartilaginous continuation of the dorsodistal end of Eb4* that articulates ventrally with the distal end of Cb5. Nelson (1967d:fig. 2j) indicated that this extension represents a partially fused Eb5 in *Engraulis* and we agree.

RDs absent.

SO longitudinal muscle layer spongy, circumesophageal, thickest dorsally, becoming extremely attenuated anterior to EO, and extending between UP4s to below anterior end of TPb4.

Additional remarks. SCL absent. TV4 anterior to Cb5s (condition relative to Bb complex not examined). Elongate anterior cartilaginous tips of Eb1s not segmented as in *Coilia*. UP4 edentate, extending dorsally as thin plate. Short, cylindrical muscle-like ligament joining ventroposterior surface of Eb1 uncinat process to ventrolateral surface of Pb2 uncinat process. Another similar ligament joining ventroposterior surface of Eb2 uncinat process to ventrolateral surface of Pb3 uncinat process.

The area between Pb2s and anterior ends of Pb3s is covered by a leathery CT sheet. The sheet attaches to the dorsalmost ends of the Pb2 uncinat processes, but the main part of the sheet lies well ventral to the dorsalmost ends, at about the level of the anterior ends of the Pb3s. The sheet apparently conforms with the ventral surface of the cranium. Mid-ventrally, the sheet incorporates a small, seed-shaped cartilage, which Di Dario (2002:500) identifies as GC, an element he first named and described in a printed journal (but see GC in Abbreviations and Definitions section): “[the engrauloid] *Cetengraulis* . . . has a typical gongyloid cartilage in *all aspects* [our italics] except that it is markedly rod-shaped . . . this shape is hypothesized as convergent to that of the [clupeid second] mediopharyngobranchial,” which Di Dario found in three of the 20 clupeid genera he examined. Di Dario followed up by allowing that in the “absence of simultaneous occurrence of the gongyloid cartilage and the second mediopharyngobranchial in any individual, the possibility of their homology cannot be conclusively discarded.” We find that the putative GC in our specimen of *Cetengraulis* (if present, it was destroyed during dissection in the other specimen) is quite dissimilar in shape, relative size, position, and in being incorporated in a CT sheet, from that of other clupeoid taxa (engrauloids, pristigasteroids) as described and illustrated by Di Dario and that we have examined. Because most (8 of 10) of the other engrauloids Di Dario (2002: table 1) examined have a GC that is typical and the other two lack GC, we think that the element in question in *Cetengraulis* is probably a modified (reduced) GC,

intermediate between character states of “full” development and complete absence.

Coilia neglecta Whitehead, USNM 357380, 2 specimens, 138–161 mm.

Plate 27

Description.

Remarks. All levators besides LI1 pass medial to LI1. LI1 is more-or-less vertical, following around the convex surface of the prootic. LI2 and LI3 pass dorsoanteriorly at about 60° and 45° angles and are “laminated” against the dorsomedial surface of LI1. LE2–4 extend anteriorly at almost 180° from their insertions.

LE1 absent.

LE2, very fine, narrowly on bony Eb2 uncinate process just distal to medial head of Eb2, which articulates with Pb2 uncinate process.

LE3 on dorsoanterior surface of Eb3 uncinate process just ventral to cartilaginous tip.

LE4 narrowly on dorsalmost edge of Eb4* just dorsal to OD4 insertion.

LP absent.

LI1 very broad, thin, on Pb2 dorsomedial margin, which is tightly bound and ventral to Pb3 slender anterior process.

LI2 thin, on Pb3 (not shown) dorsal surface posterolaterally.

LI3 thin, on Pb4 dorsolaterally.

TD comprises TPb3, TPb4-Eb3, TEb4*. TPb3, most distinct of the three, is broadly on Pb3 posterolaterally anteroventral to OD3 origin, and is posteriorly dorsal to OD4 origin and continuous by loose diagonal strands of muscle with TPb4-Eb3. TPb4-Eb3 is on Pb4 dorsolaterally just medial to LI3 insertion and medial end of Eb3 (in smaller specimen, there is slight separation of Pb4 and Eb3 sections, hence these could be accorded separate names). TPb4-Eb3 is broadly continuous posteriorly with TEb4*, which is on Eb4* dorsalmost edge ventral to OD4 insertion.

OD3 on bony dorsal surface of Pb3 uncinate process, extending a little anteriorly onto slender anterior process of Pb3, and is anteriorly dorsal to TPb3 attachment; insertion on dorsomedial edge of Eb3 uncinate process.

OD4 origin mainly on Pb3 dorsoposteriorly, with few strands on dorsoanteriormost surface of Pb4; insertion on dorsomedialmost edge of Eb4* ventral to LE4 insertion.

OP consists of strands of muscle attaching dorsally to Eb4* posteromedial surface, ventrally joining ER at mid-level of cartilaginous distal end of Eb4*; ventral to ER, apparently comprises Ad5 and SO.

Ad1–3 absent.

Ad4 on Eb4* dorsoposteriorly lateral to OP, dorsally with broad medial section separated by space from slender lateral section (nerve passes through space), ventrally on Cb4 dorsal surface medial to Eb4*-Cb4 joint.

Ad5 continuous medially with SO, dorsolaterally on distal cartilaginous end of Eb4*, ventrally on posterodistal end of Cb5, medially not separable from SO.

RD absent.

SO longitudinal muscle layer thin, spongy, circumesophageal, evenly distributed, extending dorsoanteriorly much attenuated at least to anterior end of TPb3 (possibly continuing over CT anteriorly).

Additional remarks. SCL absent. TV4 free from Cb5s, but slight attachment dorsally to ventral surface of cartilaginous Bb copula. There is an autogenous cartilage, (Plate 27A, MPb1) anterior to cartilaginous anterior tip of each Eb1 (see additional remarks under *Dussumieria*, Clupeidae). Ventral end of Pb1 attaches to dorsal surface of this cartilage. GC absent.

CHIROCENTRIDAE

Chirocentrus dorab (Forsskål), USNM 283241, 195 mm; USNM 283242, 144 mm.

Plates 28.1, 28.2

Description.

Remarks. All levators except LE1 and the muscle sheath termed LP, extend medial to LI1. LI1 is angled dorsoanteriorly at about 50–60°; the LP sheath comprises a perpendicular pyramidal section overlying or meshed with a horizontal section; the other levators are all angled horizontally at about 180°.

LE1 on tip of Eb1 uncinate process.

LE2 on tip of Eb2 uncinate process.

LE3 on medial edge of distal tip of Eb3 uncinate process.

LE4 on dorsomedialmost edge of Eb4* levator process.

LP thin, fanlike sheet of muscle fibers attached along much of lateral edge of LE4 and dorsomedial edge of Eb4*, dorsalmost fibers almost perpendicular to those of LE4.

Remarks. Greenwood and Lauder (1981:226) believed LP was absent in *C. dorab* “unless, atypically, it is closely associated with the 4th external levator . . .” We find LP is typically closely associated with LE4 in clupeoids and characoids.

LI1 posteromedially on Pb2 dorsal surface.

LI2 absent.

LI3 on lateral edge of Pb4 lateral to TPb4; appears to have two slightly separate origins.

TD comprises three parts: TPb3, TPb4, TEb4*. TPb3 on Pb3 uncinate process and Pb3 dorsolaterally posterior to uncinate process, broadest centrally, dor-

sal to OD4 origin, continuous posteriorly by few muscle strands with TPb4 in smaller specimen, not continuous in larger specimen. TPb4 broad dorsally, narrow at attachment to Pb4 just medial to LI3 insertion, continuous by diagonal muscle strap with TEb4*. TEb4* on Eb4* medially ventral to OP, continuous with SO posteriorly, but distinguishable from SO by change in direction of muscle fibers.

OD3 very small, slender, origin on Pb3 uncinat process just lateral to TPb3 attachment, insertion on posterior surface of Eb3 uncinat process ventral to LE3 insertion.

OD4 massive, origin beginning on broad dorso-posterior bony surface of Pb3 and extending onto dorsoanterior surface of Pb4, insertion on anteromedial surface of Eb4* levator process, joining raphe with OP.

OP a muscle strap and filaments attaching posteriorly on dorsomedial surface of Eb4* levator process and medial arm of Eb4*, joins raphe dorsally with OD4, inserting ventromedially among SO fibers and ventrolaterally on posterodistal surface of Eb4*.

Ad1–3 absent.

Ad4 dorsomedially on posterior surface of Eb4* levator process, ventrally narrowly on Cb4 dorsal surface just medial to inner angle formed by Eb4*-Cb4 joint.

Ad5 dorsally, narrowly on Eb4* ventrodistally; ventrally, broadly on posterior surface of Cb5; completely separate from SO medially.

RD absent.

SO longitudinal muscle layer circumesophageal, evenly distributed, extending dorsoanteriorly as sheet to below TPb4, thence as sparse filaments to below posterior end of TPb3.

Additional remarks. SCL absent. TV4 free from Cb5s. ER absent (a chirocentrid apomorphy?).

CLUPEIDAE

Dussumieria acuta Valenciennes, USNM 296827, 3 specimens, 121–123 mm.

Plate 29

Additional material. ② = *Clupea harengus* Linnaeus, USNM 325930, 106 mm; USNM 349799, 112 mm.

Description.

LE1 on cartilaginous tip of Eb1 uncinat process.

LE2 on cartilaginous tip of Eb2 uncinat process.

LE3 on cartilaginous tip of Eb3 uncinat process together with LE3' insertion, angled dorsoanteriorly similarly to LE2, attaching to cranium near LE2 attachment.

LE3' inserting on cartilaginous tip of Eb3 uncinat process together with LE3 insertion, almost horizon-

tal, extending anteriorly medial to LE1–3, attaching to cranium near cranial attachment of Pb1.

LE4 narrowly inserted on dorsoanteriormost edge of broad Eb4 levator process, continuous ventrolaterally with abruptly thinner, sheet-like LP, which is also distinguishable by abrupt change in inclination of muscle fibers. ② On Eb4*; gradual change in muscle fiber inclination between LE4 and continuous, thin LP.

LP thin, sheetlike, inserted broadly along dorsal-most edge of Eb4 levator process (lateral to insertion of LE4, but posterior given orientation of Eb4) and Eb5, continuous anteroventrally with LE4, but distinguishable by thinness and abrupt change in inclination of muscle fibers. ② broadly on Eb4*, continuous with LE4 along most of lateral edge of LE4, mainly distinguishable from LE4 by abrupt thinness of muscle-fiber sheet.

Remarks. Winterbottom (1974b:252) discussed LE4 in clupeids concluding that it was a “moot point” whether the sheet of thin muscle continuing posteriorly from LE4 could be interpreted solely as LE4 or as LP. If not as LP, he believed that LP could have evolved from a clupeid-like condition. Winterbottom (1974b:fig. 24) provided a generalized illustration of the levators in *Clupea harengus* and did not differentiate an LP. Greenwood and Lauder (1981:215) disagreed with Winterbottom's interpretation of LE4 in clupeids, “. . . we would identify the usually thin, sheet-like but somewhat expanded muscle lying ventral to [the protractor pectoralis] as the levator posterior muscle and not, as he does, a muscle composed entirely of the expanded 4th levator externus . . . even in *Clupea harengus*.” Greenwood and Lauder believed that, “Winterbottom included the posterior levator, the 4th levator externus, and some non-muscular tissue lying above and between these muscles, in the muscle he identified as the 4th levator externus.” Our observations on *Dussumieria acuta* support Greenwood and Lauder's general interpretation of LE4 and LP in clupeids, but appear to support Winterbottom's for *C. harengus*, in which the differentiation, other than a change in thickness, is unapparent.

Among pre-acanthomorphs, LP (in any form) is present only in otocephalans, and the muscle cannot be considered homologous with that of acanthomorphs.

LI1 on Pb2 dorsal surface posteromedially. ② On medial margin of Pb2.

LI2 on posterodorsal surface of Pb3, attaching to Eb2 uncinat process as muscle extends anterodorsally to origin; free from Pb1; joined by raphe with LI3 on Eb2 uncinat process (see LI3). ② At origin, attaches jointly to Pb1 and cranium; completely free from Eb2 and LI3.

LI3 on Pb4 dorsolaterally and dorsal edge of UP4

(not illustrated), fans out broadly anterodorsally, mid-anteriorly forms partial raphe with LI2 at attachment to Eb2 uncinat process. ② On dorsal surface of cartilaginous Pb4 (UP4 absent) at and medial to TD attachment to Pb4.

TD comprises TPb3-Pb4 and TEb4. TPb3-Pb4, extensive, begins anteriorly at about mid-length of Pb3s, continues posteriorly along Pb3s and Pb4s medial to, and continuous by raphe with, OD3 and OD4 origins, continuous posteriorly by diagonal muscle strands with TEb4. TEb4 on Eb4 dorsomedially, continuous posteriorly with SO by diagonal muscle strands.

② TD comprises TPb3 and TPb4-Eb4*. TPb3 short, begins just posterior to Pb3 uncinat process (well posterior to OD3origin), overlaps OD4 origin, posteriorly continuous by sparse muscle fibers with TPb4-Eb4*. TPb4-Eb4* attaches to Pb4 posterolaterally and ventromedial edge of Eb4* levator process, undifferentiated posteriorly from SO.

OD3 short, origin on Pb3 uncinat process (which joins Eb2 uncinat process), insertion on Eb3 uncinat process ventral to insertions of LE3 and LE3'. ② Long, origin on Pb3 anterior to uncinat process, fibers attach to Eb2 uncinat process as muscle passes posteriorly to insertion on Eb3 uncinat process.

OD4 origin on lateral surface of Pb3, medially joining raphe with TPb3-Pb4, fanning out posteriorly and inserting on dorsoanterior surface of Eb4 levator process, obscures insertion of OD4' on Eb4. ② Origin on posterolateralmost edge of Pb3, insertion on anterodorsalmost medial edge of Eb4* levator process; raphe absent.

OD4' origin at junction of Pb4 and UP4, extends posteriorly mostly ventral to OD4, fans out posteriorly and inserts along broad anterior surface of Eb4 levator process medial to OD4 insertion. ② Origin on Pb4 dorsoposteriorly, extends posteriorly (without fanning out) ventral to OD4 and inserts on anteromedial edge of Eb4* levator process just ventral to OD4; OD4 and OD4' more or less fused at Eb4*.

OP (not labelled), questionable area of muscle, continuous with SO, originating on Eb4 posteromedially ventral to TEb4 and joining ER posterolaterally. ② Same as *Dussumieria*, but substitute Eb4* and TEb4*; even less distinguishable in *Clupea*.

Ad1-3 absent.

Ad4 dorsally on dorsoposterior edge of Eb4 levator process and ventrally on Cb4, forming anterior wall of "pocket" separating more-or-less vertical, anterolateral continuation of SO-OP complex (see OP above), which forms posterior wall of pocket (not illustrated). ② Substitute Eb4* levator process.

Ad5 forms slender tendinous attachment dorsally to large, cartilaginous Eb5; attaches muscously to Cb5 distalmost end; undifferentiated medially from

SO ventral to ER. ② Muscously attached dorsally to Eb4* distal end.

SO with conspicuous posteromedially curving ER on each side, sheet of CT (not illustrated) arises from entire length of ER and extends posteriorly (attachment not traced). Longitudinal muscle layer begins as isolated dorsal patch at about horizontal through posterior ends of ERs (longitudinal fibers absent posterior to patch) and extends anteriorly to below TEb4 and attaches to mid-medial side of Pb4. ② ER very reduced, present on only one side of one of two specimens examined.

RD absent.

Additional remarks. SCL absent. TV4 free from Cb5, but attached mid-dorsally to Bb3. Small, unpaired, roughly U-shaped, non-staining, questionably cartilaginous pad attached to anterior ends of Pb2s dorsally. In attachments and position, U-shaped pad is faintly similar to GC of non-clupeid clupeoids. MPb1 absent. Large Eb5 present, articulating dorsally with dorsodistal end of Eb4, and ventrally with small ventrodistal end of Eb4 and broad distal end of Cb4.

② U-shaped pad absent; small, cartilaginous MPb1 present just anterior to anterior tip of each Eb1 (MPb1 reported as absent in *Clupea* by Nelson, 1967b:391, who, p. 392, implied that the unpaired MPb1- anterior to the tips of Eb1s in many clupeids, may have originated as segmentation of the cartilaginous tips of Eb1s). Eb5 absent or, by comparison with *Dussumieria*, fused with Eb4* dorsodistal end. Nelson (1967d:fig. 2b) illustrated Eb4* of *Clupea harengus* and labeled the dorsally continuous, but ventrally separate, posterior cartilaginous end of Eb4 as Eb5. He (1967b:fig. 2d) illustrated the Eb5 portion of the distal end of Eb4 in *C. harengus* as fused ventrally and separate dorsally and did not label it as separate from the remainder of Eb4. On both sides of both our specimens of *Clupea*, the ventral end is fused indistinguishably with the remainder of Eb4.

Gonorynchiformes

CHANIDAE

Chanos chanos (Forsskal), USNM 173572, 140 mm, USNM 347538, 63.3 mm.

Plate 30

Description.

LE1 on tip of Eb1 uncinat process.

LE2 on tip of Eb2 uncinat process.

LE3 absent.

LE4 originating as long tendon among other LE origins, passing medial to all other LEs, except LP, at about 180° angle, and inserting on tip of Eb4 uncinat process in larger specimen (smaller specimen lacks distinct uncinat process, and LE4 inserts on

small, dorsally raised cartilaginous process of medial head of Eb4).

Remarks. In almost all other pre-acanthomorph taxa with LE4, it originates on the dorsal margin of Eb4 (no levator process present) or on or near the LE4 levator process (including those taxa in which Eb5 is fused with the dorsodistal end of Eb4). Johnson and Patterson (1996:273) reported that *Chanos* lacks an uncinatous process, quite possibly based on examination of a small, early ontogenetic stage specimen (they did not list the size of the specimens they examined; see also illustrations of *Chanos* gill arches in Johnson and Patterson, 1996). There is a bony ridge separating the cartilaginous tip of the uncinatous process from the cartilaginous proximal head of Eb1 in our larger specimen (obscured by LE4 insertion in Plate 30). The reasons we indicate the process as an uncinatous process is that it appears to have developed as a separation of the medial head of Eb4 (Johnson and Patterson, 1996:273), and a posterior (actually lateral) levator process is present. The alternative, that two Eb4 levator processes are present is also possible, and would be uniquely synapomorphic for *Chanos*.

LP tiny, inserting on LE4 levator process well posterior to uncinatous process; origin not recorded.

Remarks. Greenwood and Lauder (1981:228) wrote that LP appeared to be absent in *Chanos*. The relatively small size of the muscle may have caused them to overlook it, or its presence may be variable. The fragile levator process was damaged on both sides of our smaller specimen during dissection and it was not possible to determine if LP was present.

LI1 on Pb2 bony surface dorsoposteriorly.

LI2 on Pb3 bony surface dorsoposteriorly.

LI3 on Pb4 dorsoanterolaterally.

TD comprises TPb3 and TEb4. TPb3 a broad band of muscle attaching to Pb3 bony dorsal surface, with slender, diagonal muscle strap extending from posterolateral end of left side and attaching to dorsal surface of Pb4 (diagonal strap absent in smaller specimen). TPb3 well separated from and not continuous with TEb4. TEb4 more extensive than TPb3, attaching to Eb4 long ventrolateral arm, continuous posteriorly with modified SO muscles.

OD3 absent.

OD4 absent.

OP indistinguishable, if present, obscured by EO. See also Ad5.

Ad1–3 absent.

Ad4 dorsally broadly on dorsoposterior edge of long ventrolateral arm of Eb4, narrowing considerably ventrally and attaching to Cb4 just medial to inner angle formed by Eb4–Cb4 joint.

Ad5 questionably represented by sheet of muscle attaching dorsally to large Eb5 cartilaginous plate and ventrally to distal cartilaginous process at end of Cb5.

Also possibly represented by muscle strap (Plate 30B, not labeled) extending from Eb5 dorsally to raphe (ER?, not labeled) on posterior surface of EO and undifferentiated from SO. Muscle sheet and/or strap possibly including OP.

SO longitudinal muscle layer circumesophageal in straight portion of esophagus (not illustrated) immediately posterior to EO; presence of SO longitudinal muscle fibers in EO problematic; fibers absent anterior to EO.

RD absent.

Additional remarks. SCL absent. TV4 well anterior to, and free from, anterior to tips of Cb5s. Pb2 and Pb3 edentulous, UP4 and UP5 absent. Eb1 with autogenous cartilaginous segment of anterior tip (MPb1) present; see discussion in additional remarks under *Gonorynchus* (Gonorynchidae).

Large, unpaired, elongate-ovate cartilage, tentatively identified as GC, present overlying anterior tips of Pb2s and Pb3s, surrounded by CT, and attaching mid-ventroanteriorly to medialmost ends of MPb1s. In so attaching, *Chanos*'s GC differs, perhaps, from that reported by Di Dario (2002), who first described GC. He reported that GC occurs only in most engrauloids and pristigasteroids among "remaining clupeiforms [= our Clupeomorpha] and basal telecephalans [= Recent Teleostei]," but did not mention its attachments. We find that it attaches to the anterior ends of the Pb2s (our observation based on pristigasteroid *Ilisha*). Di Dario's comparative material included two specimens of *Chanos*, and it would appear that if his specimens exhibited a GC-like element, he would have discussed it. His overlooking GC in *Chanos* is understandable. We failed to extract it in one of our two dissections of *Chanos* gill arches, and it appears that it has never been mentioned in any previously published study that treated the gill arches of the genus (but described by Nelson, 1966a: 157, in his dissertation).

Given the cladistic interrelationships illustrated in Fig. 3, GC in *Chanos* and GC in Clupeoidei are most parsimoniously interpreted as homoplasies, although the element may represent retention of a basal otocephalan character that has been lost independently several times.

GONORYNCHIDAE

Gonorynchus moseleyi Jordan and Snyder, USNM 354590, 231 mm.

Plate 31

Additional material. *Gonorynchus forsteri* Ogilby, USNM 353921, 90.6 mm.

Description.

Remarks. There is no substantive difference in the musculature of the two species.

LE1 on dorsoposterior edge of medialmost bony portion of Eb1, which lacks uncinat process.

LE2 on dorsoposterior surface of bony and cartilaginous medial end of Eb2, which lacks uncinat process.

LE3 minute, on cartilaginous tip of Eb3 uncinat process.

LE4 reduced, on dorsomedial edge of expanded dorsolateral cartilaginous margin of Eb4*. See also remarks following LP.

LP absent.

Remarks. Greenwood and Lauder (1981:228) reported that LP is present in *Gonorynchus*. It is possible that they identified the muscle we believe to be LE4, of which they made no mention, as LP. Unless a specimen is found that has both LE4 and LP, the identification of the muscle in question may remain unresolved.

LI1 on posteromedial surface of Pb2.

LI2 on posterodorsal cartilaginous surface of Pb3.

LI3 on posterolateral surface of cartilaginous Pb4.

TD comprises TPb3, TPb4, and TEb4*. TPb3 attaches over most of posterior half of surface of Pb3, well separated and discontinuous from TPb4. TPb4 attaches to anterodorsal surface of Pb4 and is continuous ventroposteriorly with TEb4*. TEb4* very broad, attaches to medial edge of surface of Eb4* medial arm dorsal to attachment of Ad4, and is continuous posteriorly with greatly expanded SO as it forms EO.

OD3 small, originates tendinously on bony dorsal surface of Pb3 uncinat process at lateral edge of TPb3 and inserts by slender tendon on dorsoanterior margin of cartilaginous tip of Eb3 uncinat process.

OD4 small, originates on anterolateral edge of Pb4 and inserts by slender tendon on dorsoanteriormost cartilaginous edge of Eb4*.

OP absent, perhaps highly modified by complex of CT and nerves in area between epibranchial organ laterally and esophagus medially.

Ad1–3 absent.

Ad4 on mid-posterior bony surface of Eb4* and bony dorsal surface of Cb4 medial to inner angle of Eb4*-Cb4 joint.

Ad5 apparently absent.

GFM? muscle with small portion on dorsomedial cartilaginous surface of Eb4* and long portion on dorsoposterior surface of AC (= acc of Johnson and Patterson, 1997:fig. 2b) joining Eb4* and Cb5. Interpretation highly questionable: are there gill filaments attached to AC? If not, muscle may represent separate portion of SO.

RDs absent.

SO longitudinal muscle layer (not illustrated) circumesophageal in esophagus leading into EO, continuing dorsoanteriorly as sparse fibers to at least below TPb3 and probably further.

Additional remarks. SCL absent. TV4 tripartite, divided longitudinally, with each part attaching medially to ventral surface of posterior, cartilaginous basibranchial copula to which Cb3 and Cb4 attach medially. Triangular-like cartilaginous element attaches to anterior tip of each Eb1, which Johnson and Patterson (1997:596) consider a mediosuprapharyngo-branchial (MPb1). We note that the anteromedialmost point of each MPb1 is minutely ossified where the elements of the two sides meet. Similar minute ossifications occur posteromedially where each MPb1 meets the anterior cartilaginous tip of its respective Pb2. A strong, slender ligament joins posterior edge of cartilaginous tip of Eb3 uncinat process with anterior bony edge of Eb4*. Pb2 and Pb3 edentate; UP4 and UP5 absent.

Cypriniformes

CYPRINIDAE

Zacco platypus, USNM 336890, 2 specimens, 84–101 mm; 3 cleared and counterstained, 28–82 mm.

Plates 32.1, 32.2

Additional material. © = *Opsariichthys bidens* Günther, USNM 112443, 135 mm.

Description.

Remarks. Many of the muscles described below appear to be unique to cypriniforms. Our attempts to homologize the names applied to these muscles, referring to Takahashi (1925), Holtsvoogdt (1965), and Winterbottom (1974b), were only partly successful because of unclear descriptions and illustrations. We use some of these authors' names for these muscles, but have introduced our own terminology for others. Homologies among many of the dorsal gill-arch muscles of otophysans remain to be elucidated.

LE1 on mid-posterodorsal surface of Eb1.

LE2 on mid-posterodorsal surface of Eb2.

LE3 on base of all bony Eb3 uncinat process.

LE4 on cartilaginous tip of Eb4 levator process and tiny, horizontally oriented autogenous bone (AB, Plate 32.2) attached to posterior surface of cartilaginous tip of Eb4 levator process (AB also joined by CT to pad-like insertion of LCb5A; dorsal end of Eb5 attached to AB).

LP absent.

Remarks. Winterbottom (1974b:252–253 and fig. 22) treats our LCb5 as his LP externus and our LCb5A as his LP internus. LCb5 inserts on Cb5 and LCb5A inserts on a CT pad attached to Cb5. The muscle we define as LP inserts invariably on Eb4, or joins LE4 in a combined insertion on Eb4. Furthermore, with the exception of *Chanos*, in all pre-acanthomorphs with LP, LP inserts on or together with LE4. In *Chanos*, LP inserts on Eb4 well posterior to LE4. We, therefore, infer that LP is absent in cyprini-

nids. If one or the other of these two muscles, LCb5A or LCb5, however, is derivative of the levator posterior, it would indicate that LP is a synapomorphy of the Otocephala.

LI1 on posterior surface of Pb2 dorsolaterally, near joint with Eb2.

LI2 on Pb3 mid-laterally and medial end of Eb3, which joins Pb3. ② On Pb3 mid- to posterolaterally and Eb3 and Eb4 medial ends, which join Pb3 (insertion occupying same area as combined LI2 and LI2' of *Z. platypus*).

Remarks. Takahashi (1925:41) reported that LI2 has only one insertion in *Z. platypus* (and *O. uncirostris*); the muscle is apparently variable within the genus; see also remarks under LI2'.

LI2' on posterolateral cartilaginous edge of Pb3 and anteromedial cartilaginous and bony edges of Eb4, spanning joint between Pb3 and Eb4. (see LI2). ② Not present; see LI2.

Remarks. Pb4 is absent in both *Z. platypus* and *O. bidens*, but is present in other cyprinids; e.g., New World *Notropis hudsonius* (USNM 315400, cleared and stained), Old World *Abbotina* (USNM uncat., cleared and stained). With the exception of the cyprinid genus *Pseudogobio*, which has three LIs (= our LI1, 2, 2'), Takahashi (1925:41–42) found only two LIs in cyprinoids, including *Opsariichthys uncirostris* and *Zacco platypus*. He mentions, however, that the second LI of *Cyprinus carpio* has two “caudae” [origins?]. His descriptions (p. 42) of the three LIs in cobitoids indicate very similar states to those we found for the three LIs in *Zacco platypus*.

LI3 absent.

LI4 (see LCb4).

LCb4 slender, originating on exoccipital and inserting by long tendon on Cb4 among medial fibers of Ad4.

Remarks. Holstvoogd (1965:fig. 12b) termed this muscle *levator IV internus* in the cyprinid *Leuciscus* (and also for a muscle that we term LP attaching to Eb4 in characiforms). We reserve LI for muscles inserting on pharyngobranchial elements. LCb4 occurs only in cypriniforms, possibly only cyprinids. LCb4, however, may represent a different character state for LI4, which is found only in *Diplomystes* (Diplomystidae), in which it inserts on UP4.

LCb5 massive, on dorsoposterior surface of hypertrophied Cb5, originating in subtemporal fossa with two levels of attachment: dorsoanteriorly mainly or entirely on pterotic; ventroposteriorly mainly or entirely on exoccipital; found only in cypriniforms. See remarks following LCb5A.

Remarks. Winterbottom (1974b:252–253) denoted this muscle as his LP externus (see remarks following LP above).

LCb5A small, originating in supratemporal fossa together with ventroposterior level of origin of LCb5

(q.v.), wrapping medially, then anteriorly around LCb5 and inserting in thick CT pad strongly attached dorsally to anterolateral surface of Cb5 (pad also joined anteriorly by CT to tiny AB attached to tip of Eb4 levator process).

Remarks. LCb5A appears to be the same as the internus branch of the levator posterior of Winterbottom (1974b:fig. 22b; indicated by the left line leading from his label L.POST to the muscle; the right line leads to the externus branch, which equals our LCb5).

TD absent (unique among Halecostomi); possibly replaced by thick SO section extending anteriorly ventral to pharyngobranchials.

OD3 on Pb3 bony dorsal surface anterolaterally and tip of bony Eb3 uncinat process.

OD4 on Pb3 bony surface posterolaterally and bony tip of Eb4 uncinat process.

OP absent.

RecD2 posteriorly on anteroventral surface of medial half of Eb2 and ventrolateral bony surface of Pb2, anteriorly on mid-ventromedial bony surface of Eb1.

RecD3 posteriorly on anteroventral surface of medial half of Eb3 and ventrolateral surface of Pb3, anteriorly on mid-ventromedial bony surface of Eb2.

RecD4 posteriorly on anteromedial surface of Eb4, anteriorly on bony posteromedial surface of Eb3.

Ad1–4 each attaching to ventral surface of its respective Eb and dorsal surface of its respective Cb at the internal angle formed by the two bones.

Remarks. Among pre-acanthomorphs, only polyodontids and cyprinids have Ad1–3, and their attachments in the two groups are different and different from those of acanthomorphs having Ad1–3.

Ad5 fan-like, with broad anterior end on dorso-posterior margin of Eb4 levator process and narrow posterior end on dorsolateral surface of Cb5.

RCb5T originates medially from CT and SO, well separated from contralateral RCb5T, and inserts laterally on dorsolateral margin of Cb5.

Remarks. Holstvoogd (1965:fig. 12a) called this muscle *transversus ventralis posterior*. We think the name misleading as transverses ventrales are otherwise applied to ventral gill-arch muscles. Winterbottom (1974:258; fig. 22b) identified this muscle as the retractor pharyngeus superioris.

RCb5E massive, originates on ventral basioccipital process posterior to and partially dorsal to RCb5I, and inserts on Cb5 dorsolaterally.

Remarks. Winterbottom (1974b:fig. 22) named this muscle *retractor pharyngeus inferioris*.

RCb5I relatively slender, originates as fine line of CT along dorsolateral surface of a vertical SO fold medially abutting a ventral basioccipital process and inserts by long tendon anteriorly on thick CT pad to which LCb5A (q.v.) attaches (pad attaches to Cb5).

Remarks. The vertical SO fold may be a separate muscle. It is slightly disjunct anteriorly from a posteriorly ovoid area of SO muscles, which are anteroventral to the ventral basioccipital process. A pair (one on each side) of muscle extensions continues a short distance anteriorly from the ovoid area, and these and the ovoid area muscles are covered by a tough fascia. The fascia divides and continues anteriorly on each side forming a pad covering the surface of the anterodorsal ends of Pb2 and Pb3. Anteriorly from pair of muscle extensions, the fascia forms long, slender tendons that attach to the medial surface of Pb3. Winterbottom (1974b) did not mention RCb5I.

SO longitudinal muscle layer absent at and posterior to horizontal joining posteriormost edges of Cb5s; very thick longitudinal layer begins below transverse layer anterior to horizontal and extends ventrally below gill arches well anterior to horizontal at anterior margins of Eb1s (roofs much of oral cavity); transverse muscle layer absent anterior to anteriormost external extent visible in Plate 32.1A (anterior portion of longitudinal muscle layer not overlain by transverse muscle).

RD absent.

Additional remarks. SCL absent. TV4 divided (interrupted), attached medially to each Cb5. Slender, almost threadlike cartilaginous Eb5 (may be in 1 to 3 pieces) attaches ventrally to dorsoposterior tip of Cb4 and dorsally to tiny autogenous bony element (AB) at posterodorsal tip of Eb4 levator process. Pb1, Pb4, UP4, and UP5 absent.

Characiformes

Howes (1976) treated cranial muscles of certain characiform fishes, essentially avoiding the dorsal gill-arch muscles except for mention of Kampf's (1961) brief treatment of these muscles in *Hydrocyon forskali* (= *Hydrocynus forskalii*, Alestiidae) and Winterbottom's (1974b) general study of fish musculature, which included reference to *Brycon guatemalensis* (Characidae). In apparent justification, Howes (p. 219–220) stated, "The arrangement [of the branchial muscles] in the Cynodontini is basically as in *Brycon*, and a provisional survey of branchial arch myology in . . . various characoid families (pers. obs.) suggests relative uniformity throughout the group. However, some [unspecified] specializations have been found in those taxa with epibranchial organs (*Chilodus*, *Anodus*)." There may be relatively more variation among characiform gill-arch musculature than Howes opined.

Kampf (1961:436, figs. 29–20), using terminology different from ours, reported that TD included attachment to Pb5, LE3 absent, and Ad1–3 present, character states not present in the taxa we examined.

In the case of Pb5, we find that ventral strands of SO muscle attach to the medial surfaces of UP4 and UP5. We arbitrarily did not treat the latter as part of TD, because these tooth plates extend posteriorly into the esophagus. Kampf's Ad1–3 may equal our GFM1–3. But none of the three taxa we examined lacked LE3.

CHARACIDAE

Brycon guatemalensis Regan, USNM 114526, 99.0 mm SL.

Plate 33

Additional material. ② = *Brycon melanopterus* (Cope), USNM 307072, 78.4 mm SL.

Description.

Winterbottom (1974b:fig. 20) presented a lateral view of the dorsal gill-arch muscles of *B. guatemalensis*, but some muscles are obscured.

LE1 on dorsal edge of Eb1 just lateral to cartilage tip of uncinat process; origin slightly dorsal to Pb1 articulation with skull. ② On Eb1 uncinat process just ventrolateral to cartilaginous tip.

LE2 on and just ventral to cartilaginous tip of Eb2 uncinat process. ② On Eb2 just lateral to uncinat process.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 on dorsalmost tip of Eb4 levator process and tendinous base of LP.

LP attached tendinously to dorsalmost tip of Eb4 levator process.

LI1 on dorsoposterior surface of Pb2.

LI2 on dorsal surface of Pb3 posterolaterally.

LI3 on dorsoposterior surface of cartilaginous Pb4.

TD comprises TPb3a-Eb2, TPb3p, and TPb4-Eb4 (see also discussion following Characiformes for possibly excluded TD muscle). TPb3a-Eb2 with sparse muscle strands attaching to Pb3 dorsoanteriorly, but mainly attaching to cartilaginous tip of Eb2 uncinat process laterally, posteriorly continuous by diagonal muscle strap with TPb3p. TPb3p on Pb3 posterolaterally, posteriorly continuous by diagonal muscle slips with TPb4-Eb4. TPb4-Eb4 broadly on Pb4 and narrowly on Eb4 medially, broadly continuous posteriorly with SO.

OD3 origin on Pb3 anteriorly ventral to TPb3a-Eb2, extends posteriorly dorsal to TPb3p, and inserts on cartilaginous tip of Eb3 uncinat process medial to insertion of LE3.

OD4 origin mostly on Pb4 anteriorly, slightly on Pb3 at joint with Pb4, muscle fans out posteriorly and inserts along most of lateral surface of broad levator process of Eb4.

OD4' long, slender; tendinous origin on Pb3 ventral to OD3 origin, joins OD4 insertion ventrally on anterolateral face of Eb4. ② OD4' absent.

OP a strap of muscle originating on posteromedial surface of Eb4, poorly separated from SO, ending ventrally at ER; muscle fibers continuing ventrally from ER include Ad5 and SO.

M. UP5-Cb4-Eb5 (not illustrated), origin on lateral margin of UP5, insertion at inner angle formed by Cb4 and Eb5.

Remarks. M. UP5-Cb4-Eb5 appears to be a variation of Kampf's (1961:436, fig. 30, lower right) *obliquus dorsalis inferior* in *Hydrocyon forskali* (= *Hydrocynus forskallii* (Cuvier)). Kampf described it, however, as connecting Pb5 (= our UP5?) with Cb5. Winterbottom (1974b) did not mention *obliquus dorsalis inferior* among his muscle synonymies. The albulids are the only other fishes we examined that have a possibly equivalent muscle, which we indicate as M. UP5-Cb4.

Ad1–3 absent.

Ad4 on Eb4 dorsoposteriorly and Cb4 dorsal surface medial to inner angle of Eb4-Cb4 joint.

Ad5 on Eb5 mid-posteriorly and Cb5 posteriorly, with thin dorsolateral tendinous extension (not illustrated) crossing Eb5 dorsally to distalmost bony end of Eb4; joins ER below OP laterally and SO medially, merges with SO medially and TV5 ventroanteriorly.

SO longitudinal muscle layer surrounds esophagus, thick dorsally, very thin elsewhere; fibers attaching anteriorly along medial edge of large UP4; fibers extend anteriorly to below anterior end of TPb4-Eb4. ② Layer moderately evenly distributed around esophagus.

RDs absent.

Additional remarks. SCL absent. TV4 free from Cb5s. Slender ligament from cartilaginous tip of Eb4 levator process to Eb5 dorsally. Eb5 ventrally on distalmost end of Cb4.

DISTICHODONTIDAE

Xenocharax spilurus Günther, USNM 227093, 125 mm.

Not illustrated

Description.

LE1 broadly on Eb1 uncinat process beginning a little lateral to cartilaginous tip, origin joins Pb1 articulation with skull; short, band-like tendon joins origin with Pb1 just ventrolateral to dorsal cartilage tip.

LE2 on Eb2 just lateral to tip of uncinat process.

LE3 on anteromedial edge of Eb3 uncinat process, there joining OD3 insertion.

LE4 on dorsalmost edge of Eb4 levator process, joining raphes ventrolaterally with LP insertion and Ad4 dorsally.

LP on Eb4, joining raphes ventromedially with LE4 insertion and Ad4 dorsally.

LI1 on dorsomedial surface of Pb2.

LI2 on dorsal surface of Pb3 posterolaterally.

LI3 dorsoposterolaterally on Pb4.

TD comprises TPb3a-Eb2, TPb3p, TPb4, and TEb4. TPb3a-Eb2 on Pb3 dorsally beginning at anterior edge of bony surface and extending posteriorly, and on cartilaginous tip of Eb2 uncinat process dorsally, posteroventrally continuous by diagonal muscle slip with TPb3p anteriorly. TPb3p on Pb3 posterolaterally, beginning ventral to TEb2, and just failing to meet LI2 insertion anteriorly; posteriorly continuous by diagonal muscle strand with TPb4. TPb4 broadly on Pb4, sharply separated posteriorly from TEb4. TEb4 on Eb4 anteriorly ventral to insertions of OD3–4 and OD4'.

OD3–4 origin on Pb3 anteriorly, divides posteriorly with insertions on tip of Eb3 uncinat process medial to LE3 insertion, and on Eb4 dorsolaterally.

OD4' origin on Pb4 anteriorly joining raphe dorsoanteromedially with OD3–4 origin posteriorly; insertion on Eb4 ventral to OD3–4 insertion.

OP a muscle strap originating on Eb4 posteromedially, joining TEb4 ventrolaterally and irregular ER dorsally, which is joined ventrally by Ad5 (ER continues short distance medially into SO). OP unclearly differentiated from SO medially.

M. UP5-Cb4-Eb5 origin on lateral margin of UP5, insertion at inner angle formed by Cb4 and Eb5. (Also see remarks following description M. UP5-Cb4-Eb5 in *Brycon*).

Ad1–3 absent.

Ad4 well developed on Eb4 dorsoposteriorly beginning medially ventral to uncinat process and extending laterally to end of bone, joining raphes dorsally with LE4 and LP insertions; ventrally very narrowly on Cb4 just medial to Eb4-Cb4 joint.

Ad5 bulbous, broadly on Eb5 posteriorly and Cb5 posteriorly, with thin dorsolateral tendinous extension sheathing Eb5 dorsally and attaching to distalmost bony end of Eb4; muscle joins ER ventral to OP and merges medially with SO; ventrally joins TV5 posterolaterally.

SO longitudinal muscle layer thick dorsally, very thin or absent elsewhere, begins at about horizontal connecting distal ends of Eb4s and extends anteriorly to anterior end of TEb4.

RDs absent.

Additional remarks. SCL absent. TV4 free from Cb5s. Slender ligament joins cartilaginous tip of Eb4 levator process to Eb5 dorsally, cartilage ventrally on posterodistalmost end of Cb4.

Siluriformes

DIPLOMYSTIDAE

Diplomystes chilensis (Molina)?, USNM 259097, 119 mm.

Description.

LE1 on Eb1 dorsoposteriorly.

LE2 on Eb2 dorsoposteriorly.

LE3 absent.

LE4 absent, but see remarks under LI4.

LP absent (see remarks under LI4).

LI1 on posterior margin of small CT pad, which impinges on ventral cranial surface and incorporates: medial ends of Pb1–3 and Eb1; autogenous ball of cartilage that articulates with medial ends of Eb1 and Pb2; and a few smaller autogenous cartilages; insertion splits OD3 origin.

LI2 inserts mainly on dorsoanterior edge of large UP4, with minor insertion on anterolateral cartilaginous edge of Pb4.

Remarks. Insertion of LI2 on Pb4 (or UP4) is uncommon among fishes we examined (Table 2).

LI3 medially on lateral cartilaginous edge of Pb4, ventrolaterally on UP4 dorsoposteriorly, and Eb4 medial cartilaginous cap at Eb4-Pb4 joint.

Remarks. Insertion including Eb4 is unique among fishes we examined.

LI4 originates on pterotic and inserts mainly on the dorsoposterior surface of UP4, with some fibers inserting on cartilaginous joint formed by Pb4 with Eb4.

Remarks. Takahashi (1925:67), using different terminology, considered this muscle to represent RD in siluriforms, in which it originates variously on the pterotic or supraclavicle (? = posttemporal-supracleithrum) and inserts variously on the “posterior pharyngobranchial” or Eb4 (*Diplomystes* was not among his material). Takahashi did not distinguish Pb4 from its toothplate, and we are uncertain of the exact location of the insertion in the taxa he listed. The origin of LI4 would seem to exclude interpretation of LI4 as RD, which usually originates on the anterior vertebrae, or possibly the basioccipital. Holstvoogd (1965:215 and fig. 10) termed this muscle simply “Levator IV” in the clariid siluriform *Clarias*. Winterbottom (1974b:253 and fig. 21) questionably designated the muscle LP in *Diplomystes*. Among pre-acanthomorphs, LP occurs only among Otocephala (clupeomorphs and ostariophysans), which might be evidence that the muscle we designate LI4 is a modified LE4 that has shifted its insertion from Eb4 to UP4 (the slight partial insertion including the medial end of Eb4 providing evidence). LP, otherwise, invariably inserts on Eb4 together with LE4, which *Diplomystes* otherwise lacks.

TD comprises four sections (a–d), of which the first is least differentiated. Anteriormost section, a, TPb1-Pb2-Pb3-Eb1-Eb2 (includes only anteriormost tip of Pb3) underlies pair of CT pads (see LI1) and is posteriorly continuous with next section, b, TPb3-Pb4, which joins medial bony edges of Pb3 and Pb4 and overlies anterior end of next section, c, TUP4a.

Laterally, TUP4a attaches to dorsomedial surface (ledge) of UP4, and is continuous posteriorly with d, TUP4p, which curves anteriorly and inserts along dorsolateral surface of UP4; TUP4p is continuous posteriorly with SO.

OD3 has a tripartite origin: dorsolateral origin (a) on Pb1 and posterolateralmost margin of CT pad (see LI1), including medial tip of Eb1, separated by insertion of LI1 from medial origin (b) on posteromedial margin of CT pad; these two origins, separated by LI1 insertion, meet and fuse posteriorly (obscured by recumbent LI1); ventrolateral origin (c) a short branch on Eb2, fuses with ventral surface of dorsolateral origin; complex inserts on anterior surface of Eb3 uncinete process.

OD4 origin on dorsoposterior surface of Pb3, ventral to OD3, continuing onto dorsoanteromedial surface of Pb4; insertion on anterior surface of Eb4 uncinete (levator?) process.

Remarks. Arratia (1987:11, 41) reported that *Diplomystes* lacks an uncinete process on Eb4, although mentioning that Eb4 “has a short lateral projection which I do not consider an uncinete process.” She made no mention of a levator process. We find the uncinete (or levator) process present and well developed. The uncinete process on Eb3 is armlike, whereas that of Eb4 arises vertically from the horizontal as a broad, dorsally obtuse flange with a distinct cartilaginous cap.

OP dorsally on posteromedial surface of Eb4, ventrolaterally on medial end of Eb5, ventromedially joining raphe (ER?) with SO, continuing ventrally below raphe and attaching to bony medial surface of Cb5; ventrolaterally overlapping medial portion of Ad5.

RDs absent (see LI4 above).

SO longitudinal muscle band circumesophageal, thick dorsally and ventrally, thin laterally, extending anteriorly to below anterior end of TPb3-Pb4.

Ad1–3 absent.

Ad4 dorsally on posterodorsal surface of Eb4 uncinete (levator?) process, ventrally on Cb4 dorsal surface.

Ad5 dorsally on posteromedial surface of Cb4 and ventral surface of Eb5; ventrally on dorsoposterior edge of Cb5, extending medially under OP.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 partially ossified dorsomedially. UP5 absent. Eb5 on posterodistalmost end of Cb4, horizontally oriented, a position duplicated only in *Pantodon* (Osteoglossomorpha). Small, sesamoid bone (basi-hyal?) heavily enveloped in CT present between anterior hypohyals (presumably, ventral hypohyals because they articulate with the urohyal; Arratia, 1987: fig 27, indicates these are dorsal hypohyals, whereas, Azpelicueta, 1994:figs. 6b and 11, correctly indicates they are ventral hypohyals). de Pinna (E-mail, Mar–

Apr 1999) informs us that cartilaginously tipped Eb3 and Eb4 uncinat processes occur only in *Diplomys* among siluriforms, and that the basihyal and Bb1 are absent in all catfishes.

Gymnotiformes

GYMNOTIDAE

Gymnotus carapo Linnaeus, USNM 260272, 320 mm TL.

Plate 35

Description.

Remarks. Hoz and Chardon (1984) reported on the gill-arch musculature of the gymnotid *Sternopygus macrurus*, which is very similar to that of *Gymnotus carapo*. We remark on the differences.

LE1 on Eb1 dorsoposteriorly near distal end.

LE2 posteriorly on Eb2 dorsoposterior edge just lateral to LI2 insertion, and anteriorly on dorsoposterior edge of Eb1 medial to LE1 insertion.

Remarks. Hoz and Chardon (1984) do not mention an attachment to Eb1. Verification in other specimens is desirable.

LE3 on bony Eb3 uncinat process just lateral to OD3 insertion.

LE4 on levator process at dorsodistal end of Eb4.

LP absent.

LI1 broadly, tendinously on Pb2 dorsoanteriorly and narrowly on posteromedial end of Eb1 dorsally.

Remarks. Hoz and Chardon (1984) indicate insertion only on Pb2.

LI2 primarily on dorsoanteriormost surface of medial end of Eb3, barely continuing onto adjacent lateralmost edge of Pb3, secondarily on dorsoposteriormost edge of Eb2 immediately medial to LE2 insertion.

Remarks. Identification of this muscle as LI2 is problematic because of its primary insertions on Ebs rather than Pb3. Hoz and Chardon (1984) indicate insertion is only on Eb3.

LI3 on Pb4 and UP4 dorsolaterally.

Remarks. Hoz and Chardon (1984) report insertion is only on Eb4. Their illustration (fig. 19b) is unclear, but the external position of the muscle appears similar to that of LI3 in *G. carapo*. We believe they intended to report the insertion as Pb4, a lapsus similar to their listing (p. 44) of LE4 as a [second] LE3, but labeling the muscle LE4 on their fig. 19b.

TD comprises TPb2-Pb3-Pb4 and TEb4. TPb2-Pb3-Pb4 attaches to medial edge of Pb2 on one side and to CT on other, medial edge of Pb3 (or slightly medial to edge) along OD4 origin, and Pb4 medially, and is narrowly continuous posteriorly with TEb4. TEb4 on posteromedial edge of Eb4, posteriorly continuous with SO.

Remarks. Hoz and Chardon (1984) divide TD into

two parts, one attaching to Pb2 and Pb3 and one attaching to Pb4, with no mention of an attachment to Eb4.

OD3 relatively small, originating on Pb3 dorsoanteriorly and Eb2 dorsomedialmost end, and inserting on medialmost end of bony Eb3 uncinat process.

OD4 relatively large, originating on Pb3 and Pb4 dorsally and inserting on Eb4 dorsolaterally.

OP absent.

Ad1-3 absent.

Ad4 dorsally broadly on ventrolateral surface of Eb4 and ventrally broadly on anterolateral surface of Cb4 medial to Eb4-Cb4 joint.

Ad5 ventrally broadly on posterolateralmost surface of Cb5, just impinging on lateralmost end of TV5, and dorsally narrowly on posterodistal surface of Eb5.

RDs absent.

SO longitudinal fibers circumesophageal, beginning posterior to horizontal connecting distal ends of Cb5s, forming very thick section dorsally in area between distal ends of Eb4s, and essentially absent anterior to horizontal through posterior end of TEb4.

Additional remarks. SCL absent. TV4 continuous from one side to the other, forming median raphe and attaching tightly to dorsoanteriormost tips of Cb5s. UP5 absent.

Salmoniformes

SALMONIDAE

Oncorhynchus mykiss (Walbaum), USNM 351540, 121 mm, USNM 333092, 91.8 mm.

Plate 36

Description.

LE1 on tip of Eb1 uncinat process.

LE2 on tip of Eb2 uncinat process.

LE3 on tip of Eb3 uncinat process just dorsal to OD3 insertion.

LE4 on dorsolateralmost surface of Eb4.

LP absent.

LI1 broadly on Pb2 dorsally.

LI2 on Pb3 dorsoposteriorly.

LI3 insertion enveloping Pb4 dorsal and anterior surfaces and just attaching to dorsoanterior edge of UP5.

TD a broad sheet of muscle comprising TPb3a and TPb3-Pb4-Eb4 (Pb3 portion slightly differentiated laterally from remainder). TPb3a short, laterally on Pb3 uncinat process, fusing medially with OD3 anteroventral surface dorsal to OD3'. TPb3-Pb4-Eb4 anteriorly on Pb3 ventral to OD3', forming raphe with OD4 origin, on Pb4 medial to LI3 insertion, and on medial end of Eb4, posteriorly continuous with, but noticeably demarcated from SO.

OD3 anteriorly dorsal to anterolateral portion of

TPb3-Pb4-Eb4; dorsoanteriorly on Pb3 near anterior end; joined to opposite OD3 by median raphe; another raphe lateral to median raphe setting off small wedge-like anterior muscle section; anteroventral surface joined by medial end of TPb3a, possibly evidenced by dorsolateral OD3 raphe; insertion on Eb3 uncinat process ventral to LE3 insertion.

OD3' completely ventral to OD3, origin on Pb3 posteromedial to OD3 origin and anterior to TPb3-Pb4-Eb4; fuses with ventral surface of OD3 at about mid-length of OD3.

OD4 origin on Pb3 dorsoposterior surface and Pb4 dorsoanterior surface, forming raphe with TPb3-Pb4-Eb4 medially, inserting on dorsal surface of Eb4 medial to LE4 insertion, forming partial raphe with OP and/or Ad4 dorsally; some muscle strands continuous with OP and Ad4.

OP dorsally on Eb4, ventrally joining ER at about mid-level of Eb5, below which OP is undifferentiated from SO (see also OD4). ER in smaller specimen better developed, extends medially from mid-level of Eb5 for width of OP and then turns relatively sharply posteriorly for about same distance on SO.

Ad1-3 absent.

Remarks. Dietz (1912:fig. 2; p. 19), illustrated and reported Ads1-4 in *Salmo salar* Linnaeus as follows (our translation): "This system of weak rudiments is present on the anterior four gill arches as a border of short, obliquely placed fibers along the exterior of the epibranchials and the proximal greater part of the ceratobranchials. Only against the inside of the fourth gill arch is it well developed in form . . ." Although, we did not examine *S. salar*, it is clear from his description that Dietz identified the gill filament muscles on the first three arches as adductors.

Ad4 dorsally on Eb4, ventrally on Cb4 medial to inner angle formed by Eb4-Cb4 joint (see also OD4).

Ad5 dorsally on mid-posterior surface of Eb5, and ventrally on Cb5 distal end.

RD absent.

SO longitudinal muscle layer absent posterior to horizontal between distal ends of Cb5s, present as isolated, very thick band dorsally anterior to (and above) horizontal connecting distal ends of Cb5s and continuing anteriorly only to about horizontal connecting anterior ends of Pb4s.

Additional remarks. SCL attached mid-dorsally to cartilaginous posteroventral tip of Bb3. TV4 free from Cb5s. UP4 absent.

Thymallus arcticus (Pallas), USNM 179764, 153 mm.

Plate 37

Description.

LE1 on cartilage tip of Eb1 uncinat process.

LE2 on cartilage tip of Eb2 uncinat process dorsolaterally.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 on dorsalmost edge of distal end of Eb4, between dorsal edge of OD4 insertion and dorsal attachment of Ad4.

LP absent.

LI1 on mid-dorsal bony surface of Pb2.

LI2 relatively small; on left-side muscle almost inseparable from LI3 dorsal to LI2 insertion, which is on posterodorsal bony surface of Pb3; right-side LI2 and LI3 completely separate, insertions as on left side.

LI3 on left side with two slightly separate insertions, anterior insertion on Pb4 dorsoanteriorly, posterior insertion on posterolateral edge of Pb4, continuing posteroventrally and attaching tendinously to dorsoposterolateral edge of UP5; on right side with two completely separate insertions (essentially two separate muscles), anterior muscle on dorsoanterior surface of Pb4, posterior muscle on dorsolateral edge of UP5.

Remarks. About one-fifth of left-side UP5 is ventral to Pb4 (remainder is ventral to Eb4), whereas on right side almost one-half is ventral to Pb4.

TD comprises TPb3 and TPb4-Eb4. TPb3 on Pb3 uncinat process joining raphe with anterior portion of OD3 and OD4 origins on right side and OD4 origin on left side; fibers changing from transverse to crisscross about halfway along raphe, then continuing as transverse fibers of TPb4-Eb4. TPb4-Eb4 on dorsoposterior surface of Pb4 and dorsomedial surface of Eb4, continuous with SO posteriorly.

OD3 strap-like, much smaller than OD4; left-side OD3 origin on medial edge of cartilage tip of Pb3 uncinat process ventral to OD4; right-side OD3 origin on dorsolateral surface of Pb3 uncinat process anterior to OD4 origin, but continuous posteriorly with it; insertion on both sides identical, on medial edge of cartilaginous tip of Eb3 uncinat process.

OD4 massive; left-side OD4 completely dorsal to OD3, origin begins on lateral edge of Pb3 uncinat process and continues posteriorly onto Pb4, joins raphe with TPb3; right-side OD4 origin in line and posterior to OD3 origin, joins raphe with TPb3; muscle on both sides identical, insert on dorsal surface of Eb4 medial to LE4 insertion.

OP muscle strap beginning medially on posterior surface of Eb4 and extending laterally short distance to dorsomedial edge of Ad4, barely separable medially from SO, ventrally joining ER; ventral to ER indistinguishable from SO laterally and Ad5 medially.

Ad1-3 absent.

Ad4 dorsally on posterolateral surface of Eb4 uncinat process, ventrally on Cb4 dorsal surface just medial to inner angle formed by Eb4-Cb4 joint.

Ad5 dorsally on Eb5 mid-posterolateral surface, ventrally on Cb5 posterolaterally beginning at distal

tip and extending slightly medially, medially mostly inseparable from OP.

RD absent.

SO longitudinal muscle layer absent posterior to horizontal between distal ends of Cb5s, present as isolated, very thick band dorsally anterior to (and above) horizontal connecting distal ends of Cb5s and continuing anteriorly only to about horizontal connecting anterior ends of Pb4s.

Additional remarks. SCL dorsomedially attached to posteroventral cartilaginous end of Bb3. TV4 free from Cb5s. UP4 absent. adductors.

Coregonus artedi Lesueur, USNM 117488, 2 specimens, 132–140 mm SL.

Plate 38

Description.

LE1, small, on tip of Eb1 uncinat process.

LE2 small, on tip of Eb2 uncinat process.

LE3 on tip of Eb3 uncinat process dorsolaterally.

LE4 tendinously on dorsalmost edge of distal end of Eb4.

LP absent.

LI1 on Pb2 dorsoposteriorly.

LI2 on Pb3 dorsoposteriorly.

LI3 on Pb4 dorsally.

TD comprises three parts, *a–c*: *a*, TPb3a, raised dorsally (dorsal to OD3 origin), attaching to anterior bony surface of Pb3, including anterior bony edge of Pb3 uncinat process, posteriorly continuous (discontinuous in smaller specimen) by diagonal muscle strand with more ventral TPb3p (*b*), which attaches to Pb3 bony surface dorsoposteriorly; TPb3p continuous posteriorly by broad diagonal muscle strap with *c*, TPb4-Eb4, which attaches to dorsomedial edges of Pb4 and Eb4 and is broadly continuous by diagonal band of muscle with SO.

OD3 origin divided; main portion on dorsoanterior bony surface of Pb3 ventral to TPb3a; separate, ventrolateral smaller portion (not illustrated) on posterior edge of Pb3 uncinat process; insertion on Eb3 uncinat process dorsomedially.

Remarks. Smaller specimen has undivided origin on both sides.

OD4 origin on Pb3 dorsoposteriorly and Pb4 dorsoanteriorly, insertion on dorsal edge of Eb4 well medial to LE4 insertion.

OP dorsally on Eb4 medial to Ad4 dorsal attachment; ventrally joins ER at about level of dorsal attachment of Ad5 to Eb5, and is undifferentiated from SO ventral to ER.

Ad1–3 absent.

Ad4 dorsally, broadly on Eb4 posterolaterally be-

ginning lateral to OP attachment, ventrally on Cb4 medial to inner angle formed by Eb4-Cb4 joint.

Ad5 on mid-posterior surface of Eb5 dorsally, and Cb5 distal end ventrally.

RD absent.

SO longitudinal muscle layer absent posterior to horizontal between distal ends of Cb5s, present ventrally and as isolated, very thick band dorsally anterior to (and above) horizontal connecting distal ends of Cb5s and continuing anteriorly only to about horizontal connecting anterior ends of Pb4s.

Additional remarks. SCL present. TV4 complex, attached by tendons to Cb5.

RETROPINNIDAE

Retropinna osmeroides Hector, USNM 304419, 106 mm.

Plate 39

Description.

LE1 finely, tendinously on cartilaginous tip of Eb1 uncinat process.

LE2 finely, tendinously on cartilaginous tip of Eb2 uncinat process.

LE3 on tip of Eb3 uncinat process.

LE4 on dorsodistal edge of Eb4*.

LP absent.

LI1 on Pb2 dorsoposteromedially ventral to anterior end of Pb3.

LI2 on Pb3 dorsoposteriorly (well separated from LI3 insertion on Pb4).

Remarks. Right-side LI2 probably anomalous, has slender separate portion inserting on Pb4 anteriorly, and well separated from main LI2 and LI3 insertions.

LI3 on Pb4 dorsoposteriorly.

TD comprises TPb3a and TPb3p-Pb4-Eb4*. TPb3a lies dorsal to remainder of TD, comprises loose strands of muscle connecting bony lateral edges of Pb3 uncinat process dorsal to origin of OD3, connected posteriorly by fine muscle strand to TPb3p-Pb4-Eb4*. TPb3p-Pb4-Eb4* broad, compact, attaches to Pb3 dorsal surface dorsoposterolateral to OD4 origin, and to medial surfaces of Pb4 and Eb4*.

OD3 origin on Pb3 dorsoanteriorly ventral to TPb3a, insertion on tip of Eb3 uncinat process ventromedial to LE3 insertion.

OD4 origin on Pb3 posterodorsal bony surface ventral to posterior margin of TPb3p portion of TPb3p-Pb4-Eb4*, insertion mostly on Eb4* dorso-lateral edge proximal to LE4 insertion.

OD4' fine, originating on Pb4 dorsal surface completely ventral to OD4; originating fibers pass through TPb3p-Pb4-Eb4*; muscle fuses with OD4 ventral surface well anterior to OD4 insertion.

Remarks. Muscle is possibly anomalous; confirmation of its presence in other specimens is desirable.

OP comprises two or three muscle strands origi-

nating on posteromedial surface of Eb4* dorsal to SO attachment to Eb4*, joining ER dorsally, undifferentiated from SO ventral to ER.

Ad1–3 absent.

Ad4 dorsally on posterior surface of Eb4*, ventrally on Cb4 dorsal surface just medial to inner angle formed by Eb4*-Cb4 joint.

Ad5 dorsally on posterodistal surface of cartilaginous Eb4* posterodistal hook-like process, ventrally on posterodistal surface of Cb5, medially continuous with SO or OP?

RD absent.

SO longitudinal muscle layer absent or represented at most by few sparsely distributed fibers dorsally and ventrally posterior to horizontal through distal ends of Cb5s, dorsally becoming thick, then attenuating, and extending anteriorly to anterior end of TD.

Additional remarks. SCL absent. TV4 absent.

GALAXIIDAE

Galaxias auratus Johnston, USNM 344888, 85.6 mm.

Plate 40

Description.

LE1 on mid-posterior edge of Eb1, attaches to dorsal tip of Pb1 at origin.

LE2 on mid-posterior edge of Eb2.

LE3 tiny, jointly with OD3 insertion on cartilaginous tip and lateral edge of Eb3 uncinat process.

Remarks. LE3 reduced relative to LE1 and LE2, similar to *Lovettia*.

LE4 dorsodistally on Eb4* with posterodistal strand extending ventrally and attaching to ventro-posterior surface of Eb4* distal end.

LP absent.

LI1 on Pb2 dorsal surface anteromedially.

LI2 on Pb3 dorsal surface posteromedially.

LI3 on Pb4 dorsal surface.

TD undifferentiated sheet of muscle comprising TPb3-Pb4-Eb4*, attaching to Pb3 medial to OD origins, Pb4 medial to LI3 insertion, and medial end of Eb4*.

OD3 and OD4 are bilaterally asymmetrical. OD3 originates dorsally on cartilaginous anterior end of Pb3 on both sides. Left-side origin well separated anteriorly from OD4 origin on Pb3 bony dorsal surface, insertion on Eb3 cartilage-tipped uncinat process medial to and together with LE3; however, strand of muscle at anterior end of OD4 origin (well separated posteriorly from OD3 origin) also inserts with OD3. Right-side OD3 origin and insertion similar to left-side, but strand of muscle originates at posterior end of origin and inserts on Eb4* together with OD4 insertion. Right-side OD3 origin, except for strand, also well separated from OD4 origin.

OD4 origin on both sides, except for strand on left

side, from multiple separate muscle strands on Pb3 bony dorsal surface, combining to insert on Eb4* dorsodistal end medial to LE4 insertion.

OP muscle band originating dorsally on dorsomedial edge of Eb4*, questionably separate dorsomedially from SO, joining ER dorsally at mid-posterior level of Eb4* distal end; undifferentiated from SO ventral to ER.

Remarks. Configuration of OP, Ad5, SO, and ER similar to that of *Lovettia*.

Ad1–3 absent.

Ad4 dorsally, broadly on posterior edge of Eb4*, ventrally on Cb4 medial to inner angle formed by Eb4*-Cb4 joint.

Ad5 broadly on posterodistal end of Cb5, dorsally narrowly attaching to mid-posterodistal end of Eb4*, medially indistinguishable from SO.

RDs absent.

SO longitudinal muscle layer absent posterior to horizontal between distal ends of Cb5s, present as isolated thick muscle band dorsally anterior to (and above) horizontal connecting distal ends of Cb5s, and continuing anteriorly only to about horizontal connecting medial ends of Eb4s*.

Additional remarks. SCL absent. TV4 attached to Cb5. Several tiny accessory cartilages on each side of gill arches. Small cartilage just anterior to anterior cartilaginous tip of Pb3 on both sides (possibly representing a segmentation of the anterior tips of Pb3). Anteriormost AC on left side between Eb1 cartilaginous medial end and anterior cartilaginous end of Pb2 just anterior to bony portion; anteriormost on right side between medialmost tip of Eb1 and adjacent cartilaginous edge of Pb2; posteriormost cartilage on left side filamentous, parallels posteromedial edge of Pb2; posteriormost (not illustrated) on right side, very tiny, between cartilaginous tips of Pb3-Eb3 joint. Eb1 and Eb2 lack uncinat processes.

Lepidogalaxias salamandroides, USNM 358461, 43.7 mm; Murdoch University, 47.3 mm.

Plate 41

Description.

Remarks. The muscles are highly modified and confusing. Our interpretations of TPb3, OD3, OD4, and OD4' are provisional.

LE1 on Eb1 bony surface dorsodistally.

LE2 on Eb2 at base and lateral to uncinat process.

LE3 on dorsodistalmost end of Eb3 and ligament (not shown) extending from insertion to distal end of Cb4.

LE4 on anterodistal surface of Eb4, muscle in cross section V-shaped with apex directed medially.

LP absent.

LI1 on dorsoposterior surface of Pb2.

LI2 absent.

LI3 unusually large, on Pb4 dorsally, insertion ending posteriorly at margin of Pb4 with UP5? (not shown).

Remarks. In the larger specimen, LI3 also appears to be attached to UP5?, but damage during dissection leaves this observation problematic.

TD appears to comprise only broad TPb3, which attaches on Pb3 dorsally, joining raphe anterolaterally with OD3, extending posteriorly as complexly oriented fibers, interrupted by irregular, somewhat median raphe, and joining another raphe on each side medial to LI3. OD4' appears to originate at latter raphe.

OD3 passes lateral to LI3, origin on Pb3 anterior end, joining raphe there with TPb3, insertion on Eb3 dorsodistally.

OD4 a muscle strap originating on Eb3 along raphe with OD3 and attaching to Eb4 dorsodistally between insertion of LE4 and OD4'.

Remarks. This muscle could be interpreted as a RecD4, but other than its origin on Eb3, an apparent slight shift laterally from the highly reduced, tiny, rod-like, edentate Pb3, its insertion is fairly typical of OD4, and the relationship with OD3 is reminiscent of the more-or-less in-line origins of OD3 and OD4 in other pre-acanthomorphs.

OD4' appears to originate at a raphe with TPb3 and, on one side, RD well medial to LI3, and is interrupted by another raphe immediately medial to LI3 before attaching to dorsal surface of Eb4 just medial to OD4. OD4' lies dorsal to unnamed band of muscle attaching anteriorly to posteromedial surface of Eb4 and joining raphe posteriorly with RD. We were unable to determine if OD4' attaches to Pb4 or UP5.

OP dorsally on Eb4 posterior edge medial to Ad4 dorsally, muscle ending ventrally at ER, which continues laterally along dorsal end of Ad5, becoming tendinous and attaching to Eb4 posteroventrally and Cb4 posteriorly (ER tendinous attachments to Eb4 and Cb4 (obscured on Plate 41); OP undifferentiated from SO medially.

Ad1–3 absent.

Ad4 dorsally on Eb4 posterolaterally, ventrally on Cb4 medial to Eb4–Cb4 joint.

Ad5 on Cb5 posterodistally, joining ER dorsally, and forming tendinous attachment to Eb4 and Cb4.

SO longitudinal fibers absent anterior to horizontal through posterior ends of Eb4s, unless represented by RDs; condition of specimen precluded determination of posterior extent, unless indicated by posterior ends of RDs.

SOD absent.

RDs completely external to SO, broadly inserted on raphe with unnamed muscle band on one side and with muscle band and OD4' on other side.

Additional remarks. SCL absent. TV4 divided, free

from Cb5, medial end of each division attaching to ventral surface of bony Bb4. Eb1 and Eb3 lack uncinuate processes. UP4 questionably absent. Eb4 and Cb4 appear to have unmodified distal cartilaginous ends (see also Rosen, 1974:fig.15B), with no trace of Eb5.

Lovettia sealei (Johnston), USNM 358617, 2 specimens, 50.2–54.2 mm.

Plate 42

Description based primarily on smaller specimen.

LE1 on Eb1 dorsoposterior edge somewhat medial to mid-length of bone.

LE2 weakly developed (easily overlooked or destroyed), on Eb2 dorsoposterior edge somewhat medial to mid-length of bone.

LE3 greatly reduced, on finger-like dorsal extension (modified, displaced uncinuate process?) of cartilaginous distal tip of Eb3.

Remarks. LE3 reduced relative to LE1 and LE2, similar to *Galaxias* LE2.

LE4 on Eb4* dorsodistally.

LP absent.

LI1 on Pb2 dorsomedially.

LI2 on Pb3 dorsoposteriorly.

LI3 on Pb4 dorsoposteriorly.

TD not clearly partitioned, comprises TPb2–Pb3–Pb4–Eb4*, beginning as few muscle strands on Pb2, continuing posteriorly onto Pb3 and Pb4, and medial ends of Eb4*, slightly differentiated posteriorly from SO.

OD3 origin on Pb3 dorsoanteriorly, insertion on dorsomedialmost edge of finger-like extension of cartilaginous distal tip of Eb3.

OD4 on Pb3 dorsoposteriorly and Pb4 dorsoanteriorly, with slight separation of muscle between Pbs; insertion on dorsomedialmost cartilaginous edge of distal end of Eb4*.

Remarks. Left-side OD4 of larger specimen has split origins on Pb3.

OP relatively small strap of muscle dorsally on posterior surface near medial end of Eb4*, joining ER ventrally, not distinguished from Ad5 or from SO below ER.

Remarks. Configuration of OP, Ad5, SO, and ER similar to that of *Galaxias*.

Ad1–3 absent.

Ad4 on dorsoposterior surface of Eb4*, ventrally on Cb4 anterior to inner angle formed by Eb4* and Cb4.

Ad5 on mid-distal end of Eb4* and posterodistal end of Cb5, not separable medially from SO and/or OP.

SO, unable to determine by gross dissection if longitudinal muscle layer is present.

RDs absent.

Additional remarks. SCL absent. TV4 divided, free from Cb5, medial end of each side attached to ventral surface of Bb3. Eb1, Eb2, and Eb3 uncinat processes absent. UP4 and UP5 absent.

OSMERIDAE

Hypomesus pretiosus (Girard), 2 specimens, USNM 357404, 135 mm; USNM 70839, 172 mm.

Plate 43

Additional material. ② = *Mallotus villosus*, USNM 104700, 148 mm.

Description.

Remarks. The levators of the smaller *Hypomesus* specimen have relatively long tendinous origins, whereas the origins of the larger specimen (and those of *Mallotus*) are relatively short and mostly muscular.

LE1 slender, on dorsodistal edge of Eb1 uncinat process.

LE2 slender, on dorsal tip of Eb2 uncinat process.

LE3 on dorsal tip of Eb3 uncinat process.

LE3', thin, applied closely to anterior surface of LE3, insertion on Eb3 uncinat process just ventral to LE3 insertion.

Remarks. The flat "anterior" surface of LE3 is positioned parallel to the body midline, as is usual in fishes, and the flat surface of LE3' is applied ("laminated") to the flat surface of LE3. The muscles originate together and their distinction might escape casual examination.

LE4 originates in cluster with other LEs; inserts on dorsalmost edge of Eb4* levator process.

LE4' very slender, closely applied for almost entire length to distal edge of LE4, origin not diverging much from that of LE4, insertion along edge of LE4. ② Origin diverging slightly but noticeably from that of LE4, but attached for most of length to distal edge of LE4, becoming tendinous toward insertion.

Remarks. Not considered LP because origin is with clustered LEs.

LP absent.

LI1 on dorsoposterior surface of Pb2.

LI2 on dorsomedial surface of Pb3 posterior end, at and lateral to attachment of TPb3p.

LI3 on Pb4 dorsal surface at and lateral to TPb4-Eb4* attachment.

TD comprises three parts: TPb3a-Eb2, TPb3p, and TPb4-Eb4* (described separately for *Mallotus*). TPb3a-Eb2 most distinct, dorsally situated relative to remainder of TD, with lateral attachments to joined tips of Pb3 and Eb2 uncinat processes, and crossed lateral attachments to dorsoanterior Pb3 bony surfaces dorsal to OD3 origins, completely separate from TPb3p in larger specimen, continuous posteriorly by

diagonal fiber bundle with TPb3p in smaller specimen. TPb3p on Pb3 dorsal surface posterior to uncinat process and medial to LI2 insertion, continuous by diagonal muscle fibers with TPb4-Eb4*. TPb4-Eb4* on Pb4 dorsolaterally medial to LI3, and on dorsomedial edge of Eb4, posteriorly almost inseparable posteriorly from SO.

② Comprises TPb3a, TPb3p, and TPb4-Eb4*. TPb3a on Pb3 uncinat process laterally, ventromedially attached to CT between well-separated anterior ends of Pb3s (Pb3s of *Hypomesus* almost impinge along medial edges), no crossed lateral attachments to Pb3s dorsoanteriorly dorsal to OD3 origin, dorsally situated relative to remainder of TD, continuous posteriorly with TPb3p posteriorly. TPb3p on Pb3 laterally posterior to uncinat process, continuous posteriorly with TPb4-Eb4*. TPb4-Eb4* on Pb4 dorsolaterally and Eb4* medially, posteriorly distinguished from SO by change in muscle fiber direction.

OD3 origin on dorsoanterior bony surface of Pb3 ventral to TPb3a-Eb2, insertion on Eb3 uncinat process medial to LE3 and LE3' insertions. ② Origin ventral to TPb3a.

OD4 origin on posteriormost end of Pb3 and dorsoanterior surface of Pb4, insertion on medial edge of Eb4*. ② OD4 origin on Pb3 dorsoposteriorly and OD4' on Pb4 dorsoanteriorly, muscles joining just posterior to OD4' origin, but somewhat (artificially?) separable for entire length, with OD4 inserting on Eb4* dorsoanteriorly and OD4' inserting on medial edge of Eb4* ventromedial to OD4.

OD4' absent. ② Anteriorly on Pb4 dorsoanteriorly and posteriorly on Eb4* medial edge; just posterior to origin, joins OD4, but is somewhat separable (artificially?) for entire length.

OP strap of muscle dorsally on dorsomedial edge of Eb4*, partly dorsal to attachment of TPb4-Eb4* to Eb4*; ventrally joins ER with SO; indistinguishable ventral to ER.

Ad1-3 absent.

Ad4 dorsally on dorsoposterior edge of Eb4*, ventrally on Cb4 just medial to inner angle formed by Eb4*-Cb4 joint.

Ad5 on posterodistal end of Eb4* and posterodistal end of Cb5, weakly separable from SO (or OP?) medially. ② On posteriorly extending finger-like cartilaginous extension of Eb4* distal end and posterodistal end of Cb5.

RDs absent.

SO longitudinal fibers begin well posterior to horizontal through posterior ends of Cb5s and continue anteriorly to horizontal between anterior ends of Pb4s (posterior to TPb3p).

Additional remarks. SCL attached posteromedially to ventroposterior cartilaginous tip of Bb3—ligament almost circular with massive muscle attachments; ② SCL absent. TV4 free from Cb5s, divided at mid-

line, attaching dorsally to ventral surface of Bb series (specific element not determined). Smaller specimen with two tiny ACs just anterior to anteroventral surface of Pb1 on left side, one on right side; larger specimen with one AC (not illustrated) on right side only. Johnson and Patterson (1996:277) discuss problems concerning the identification of the upper pharyngeal tooth plate, or plates, as representing UP4 or UP5, but appear to favor identifying it as UP5.

The posterior end of Eb4 has the foramen for the fifth efferent artery bordered completely by bone anteriorly and by cartilage posteriorly in the larger specimen of *Hypomesus*; the cartilaginous portion is interrupted in the middle in the smaller specimen (see Rosen, 1974:fig. 16D). The posterior end of Eb4 in the specimen of *Mallotus* is similar to that of the larger specimen of *Mallotus* except that there is a very fine joint line (both right and left arches) between the dorsomedial end of "Eb5" and the dorsolateral cartilaginous end of Eb4. The condition in our experience is exceptional. Eb5 usually appears to fuse to Eb4 dorsally first, and ventrally last (see comments on clupeomorphs by Rosen, 1974:280). Rosen (1974:284), however, states that the opposite is true for osmeroids: fusion takes place ventrally first; however, he provided no evidence for this. Based on his illustrations of the osmeroid taxa (his fig. 16), all have either a free Eb5 or a fused Eb5 that can be interpreted alternatively as having had Eb5 fused completely with Eb4 and subsequently variously and partially lost, with no unequivocal indication whether fusion took place dorsally or ventrally first.

Argentiniformes

ARGENTINIDAE

Argentina brucei Cohen and Atsides, USNM 238005, 99.5 mm.

Plate 44

Description.

LE1 on Eb1 at and just lateral to base of uncinat process.

LE2 on dorsolateral edge of Eb2 uncinat process.

LE3 on dorsolateral edge of Eb3 uncinat process.

LE4 on dorsolateralmost tip of Eb4 levator process just dorsal to insertion of OD4 anteriorly and dorsal attachment of Ad4 posteriorly.

LP absent.

LI1 on Pb2 mid-dorsally.

LI2 on Pb3 dorsoposteriormost bony surface, beginning just lateral to OD4 origin.

LI3 on Pb4 dorsoposteriorly.

TD long, broad, essentially undifferentiated, comprising TPb3-Pb4-Eb4, which attaches along dorso-medial surfaces of Pb3 and Pb4 and meeting insertions of OD3 and OD4, and with narrow attachment

to posteromedial edge of Eb4; posteriorly continuous with SO.

OD3 origin mid-dorsally on Pb3 just medial to LI2 insertion, insertion on Eb3 uncinat process ventroanterior to LE3 insertion.

OD4 origin broadly on Pb3 beginning at posterior end of OD3 origin, insertion on Eb4 levator process ventroanterior to LE4 insertion.

OP strap of muscle overlying SO dorsolaterally, dorsally on Eb4 posteromedial surface, ending ventrally at ER (right side ER very weak), scarcely separable ventrally from Ad5 and SO.

Ad1-3 absent.

Ad4 dorsally on posterodorsal surface of Eb4, ventrally on dorsal surface of Cb4 anterior to inner angle formed by Eb4-Cb4 joint.

Ad5 dorsally on mid-distal surface of Eb5, ventrally on posterodistal bony surface of Cb5 ventrally, forming raphe with posterolateral end of TV5, medially continuous with SO.

SO with strap of muscle arising laterally, extending dorsally, then ventrally and attaching to anterior surface of Eb5 to form wall of pocket lined anteriorly by Ad4; continuous ventrolaterally with Ad5 (or ?OP). Longitudinal fibers commencing well posterior to horizontal between distal ends of Cb5s and continuing anteriorly, thinly to horizontal connecting medial ends of Eb3.

RD absent.

Additional remarks. SCL absent. TV4 free from Cb5s. Eb5 large, on dorsodistal end of Cb4, articulating ventroanteriorly with posterodistal end of Eb4, attached dorsally by long, slender ligament to Eb4 levator process. Accessory cartilage on dorsodistal end of Cb5, surrounded by tubular CT, which is attached to mid-posterior surface of Eb5.

ALEPOCEPHALIDAE

Alepocephalus tenebrosus Gilbert, USNM 215582, 141 mm.

Plate 45

Description.

Remarks. LE1 and LIs together surround and attach to dorsal end of very long, slender SPb1 and to cranium; LI1 also attaches along dorsomedial surface of SPb1.

LE1 slender, on dorsolateral edge of Eb1 uncinat process.

LE2 slender, on dorsodistal edge of cartilaginous medial end of Eb2.

Remarks. Medial cartilaginous end of Eb2 expanded dorsally, and dorsally does not articulate with Pb3; Eb2 uncinat process absent, unless modified dorsal expansion of medial end represents shift in position of uncinat process.

LE3 slender, on cartilaginous tip of Eb3 uncinat process.

LE4 very slender, inserts finely, tendinously on mid-dorsal cartilaginous edge of distal end of Eb4.

LP absent.

LI1 broadly on bony dorsal surface of Pb2, dorsally on SPb1 beginning a little ventral to attachment to skull and continuing to muscle origin.

LI2 slender, on dorsal surface of bony and cartilaginous posterior end of Pb3.

LI3 from single origin, spreads ventrally, becoming fan-like and inserting on Pb4 as group of separated muscle strands; on right side only, anteriormost muscle strand is also attached to cartilaginous medial tip of Eb3.

TD comprises short TPb3a, much longer TPb3p-Pb4, and short TEb4. TPb3a attaches to bony dorsal surface of Pb3 anterior processes and is noticeably distinct, although broadly continuous posteriorly with TPb3p-Pb4. TPb3p-Pb4 attaches along the dorso-medial margins of Pb3 and Pb4 and is broadly continuous posteriorly with TEb4, although separated from TEb4 by a posterolateral notch in the muscles at the posterior end of Pb4 and anterior end of Eb4. TEb4 attaches along anteromedial margin of Eb4 and becomes continuous posteriorly with SO by broad area of crisscrossing muscle fibers.

OD3 slender, origin on medial surface of Pb3 uncinat process, with fibers extending anteriorly and joining posterolateral edge of TPb3; insertion on dorsoanteriormost edge of Eb3 uncinat process.

OD4 slender, origin on posteroventral edge of Pb3 uncinat process ventral to OD3 origin; tendinous insertion on dorsoanterior cartilaginous edge of Eb4, continuous at insertion with OD4' insertion.

OD4' slender, origin on anterodorsal surface of Pb4; insertion on Eb4 continuous with OD4 insertion.

OP absent, but possibly represented by stringy muscle strands attaching to posteromedial surface of Eb4; strands become complexly meshed posteroventrally with SO muscle strands (complexity not illustrated). ER absent, but possibly represented by area where problematic OP muscle strands mesh with SO strands.

Ad1-3 absent.

Ad4 on posterior surface of dorsodistal end of Eb4 and dorsoposterior surface of Cb4 at internal angle formed by Eb4-Cb4 joint.

Ad5 attaching cartilaginous Cb5 distal end posteriorly to ventral margin of large Eb5.

SO longitudinal fibers loosely incorporated in fluffy brown matrix beginning well posterior to horizontal between posterior ends of Cb5s, and decreasing in density abruptly at horizontal between anterior ends of Eb4s; very thin matrix, possibly including

sparse muscle fibers, continuing into pharyngeal area anterior to gill arches.

RDs absent.

Additional remarks. SCL absent. TV4 free from Cb5s. Cartilaginous end of Pb1 ventromedial process articulating with anterior end of Pb2, ventrolateral cartilaginous end articulating with anterior cartilaginous end of Eb1. Pb1 and tips of Pb2 and Pb3 enveloped in loose CT pad (not illustrated); pad attached posteriorly to long, slender ligament, which joins contralateral ligament at attachment to cranium.

Large Eb5 present posteriorly, articulating ventrally with dorsal edge of posterior ends of Cb4 and Eb4; large AC articulating ventrally with Cb5 and Eb5 medially; right side only with two additional tiny accessory cartilages laterally on Eb5. SPb1 present.

There is great similarity in the shapes and "lay-out" of the muscles of *Alepocephalus* and *Searsia*, especially when compared with their sister group, *Argentina*.

PLATYTROCHTIDAE

Searsia koefoedi Parr, USNM 206873, 117 mm.

Plate 46

Description.

Remarks. LE1 and LIs surround and attach to SPb1 ventral to origins on cranium (all levators originate together on cranium).

LE1 slender, inserts by slender tendon on dorso-posterior edge of Eb1 lateral to uncinat process.

LE2 absent.

LE3 slender, on cartilaginous tip of Eb3 uncinat process.

LE4 very slender, finely, tendinously on mid-dorsal cartilaginous edge of Eb4.

LP absent.

LI1 broadly on dorsomedial surface of bony portion of Pb2, dorsally on SPb1 near insertion on skull; posteroventral fibers of left-side LI1 attach (anomalously) to lateral edge of Pb3.

LI2 on posterodorsal surface of Pb3; right side with few fibers attaching to anteriormost surface of Pb4, dorsally difficult to separate from LI3'.

LI3 on Pb4 posterolaterally; lightly attached to medial surface of SPb2.

LI3' slender, but moderately broadly on Pb4 dorsoanteriorly lateral to origin of OD4'; right side LI3' both anterior and lateral to origin of OD4', dorsal fibers not clearly separable from LI2.

TD comprises short TPb3a, which attaches to bony Pb3 anterior process, and much longer TPb3p-Pb4-Eb4, which attaches along dorsomedial edges of Pb3, Pb4, and Eb4, and is broadly continuous with SO posteriorly.

OD3 origin on medial surface of Pb3 uncinat process; insertion on dorsomedialmost edge of Eb3 un-

cinate process; left side OD3 lies dorsal to and almost completely hides OD4; right-side hides all but anterolateralmost OD4.

OD4 origin with and ventral to OD3 origin on Pb3 uncinete process; insertion on dorsomedial cartilaginous edge of Eb4, continuous posteriorly with posterior portion of OD4'.

OD4' origin on anterodorsal surface of Pb4; left side fuses with OD4 at about mid-length; right side fuses with OD4 just anterior to insertion on Eb4.

OP absent, but possibly represented by stringy muscle strands attaching to posteromedial surface of Eb4; strands become complexly meshed posteroventrally with SO muscle strands (complexity not illustrated). ER absent, but possibly represented by area where problematic OP muscle strands mesh with SO strands.

Ad1–3 absent.

Ad4 on dorsomedial surface of Eb4 and postero-dorsal surface of Cb4 at inner angle formed by Eb4-Cb4 joint.

Ad5 narrowly on Eb4 ventrodistally and broadly on Cb5 ventrodistally; right side with few fibers attaching to AC.

SO longitudinal fibers loosely incorporated in fluffy brown matrix beginning well posterior to horizontal between posterior ends of Cb5s, decreasing in density and ending abruptly, or nearly so, at about horizontal between posterior thirds of Pb4s (matrix, at least, continuing anteriorly into pharyngeal area anterior to gill arches).

RDs absent.

Additional remarks. SCL present with dorsomedial CT pad attaching to Bb3 posteroventral tip. TV4 free from Cb5s. Pb1 with cartilaginous end of ventromedial process articulating with anterior tip of Pb2; ventrolateral process with two separated cartilaginous tips, articulating with anterior cartilaginous tip of Eb1. Pb1 and tips of Pb2 and Pb3 enveloped in tough CT pad. Eb5 articulating laterally with Eb4 and medially with AC, which articulates ventrally with Cb5.

Cartilaginous SPb1 on dorsal cartilaginous tip of Eb1 uncinete process, SPb2 on dorsal cartilaginous tip of Eb2 uncinete process. Johnson and Patterson (1996:275) reported that *S. koefoidi* has only SPb1. Their report was based on SIO 77-38 and 77-53 (Johnson and Patterson, 1996:323), collected in the Banda and Sulu seas, whereas our specimen was collected in the northeastern Atlantic (type locality, however, is Bahamas). Matsui and Rosenblatt (1987:73) reported that, "the width of the frontals differs between *S. koefoedi* of the 3 ocean regions." It appears likely that more than one species is involved.

There is great similarity in the shapes and "lay-out" of the muscles of *Alepocephalus* and *Searsia*, especially when compared with their sister group, *Argentina*.

Esociformes

ESOCIDAE

Esox niger Lesueur, USNM 355803, ca. 235 mm.

Plate 47

Additional material. ② = *Esox lucius* Linnaeus, USNM68894, 87.5 mm.

Remarks. Poor condition of *E. lucius* specimen provided only limited amount of information, but no noteworthy differences were observed in the muscles of the two species.

Description.

LE1 broadly, fibrotendinously on cartilaginous cap of Eb1 uncinete process.

LE2 on tip of Eb2 uncinete process.

LE3 on tip of Eb3 uncinete process.

LE4 absent.

LP absent.

LI1 massive, broadly on Pb2 bony surface dorso-medially.

LI2 broadly on Pb3 bony surface dorsoposteriorly.

LI3 on Pb4 dorsomedial surface.

TD comprises TPb3a and TPb3p-Pb4. TPb3a attaches along lateral edge of anterior half of Pb3, is dorsal to origin of OD3, and posteriorly continuous by diagonal strand of muscle with TPb3p-Pb4. TPb3p-Pb4 attaches to Pb3 and Pb4 dorsal surfaces medial to insertions of LI2 and LI3, joins dorsolateral raphe with OD4 origin, with which TPb3p-Pb4 is otherwise continuous, and is also continuous posteriorly with SO.

OD3 origin on dorsal surface of Pb3 ventromedial to attachment of TPb3a, insertion on Eb3 uncinete process proximal to LE3 insertion.

OD4 absent. See remarks following OD4'.

OD4' originates dorsally from raphe with TPb3p-Pb4 and ventrally from Pb4 dorsal surface, and inserts on Eb4 uncinete process.

Remarks. OD4' of *Esox* is similar to OD4' of the putatively related *Novumbra*, particularly in that both have their main origins on Pb4 rather than Pb3. *Novumbra* has OD3–4 fused or separate (OD3 and OD4) as well as OD4'.

Johnson and Patterson (1996:275) argued that esocoids may have an uncinete process, but not a levator process. As far as we know, an Eb4 levator process never articulates with the Eb3 uncinete process, whereas, the Eb4 uncinete process usually, if not always, does, thus supporting the Johnson and Patterson's interpretation of the process in *Esox*. The presence of an Eb4 uncinete process, and its articulation with the Eb3 uncinete process, in *Esox* is either an autapomorphy of *Esox*, or evidence that its closest relationships are with the basal acanthomorphs, in which these states first occur.

OP indistinct, probably represented dorsally by muscle attaching to posterior surface of Eb4 beginning ventral to uncinat process and extending medially, and ending ventrally at ER on Cb4, there joined by Ad5 dorsally. This configuration OP, ER, and Ad5 also appears in *Saurida* (Synodontidae) and some acanthomorphs, e.g., *Polymixia*.

Ad1–3 absent (condition of GFM's not determined).

Ad4 dorsally appears to attach along entire posterior surface of Eb4, although medial half probably represents OP, which ventrally joins ER with Ad5.

Ad5 on Cb5 distally and bony posterior surface of Cb4, where it joins ER dorsally with presumable OP ventrally.

RDs absent.

SO longitudinal muscle layer originates well posterior to gill arches and extends anteriorly to horizontal at anterior ends of Pb4s, abruptly decreasing or vanishing anterior to horizontal.

Additional remarks. SCL attached dorsomedially to posteroventral cartilaginous end of Bb3. TV4 free from Cb5s (completely anterior to anterior tips of Cb5s). UP5 absent. Eb 5 absent.

UMBRIDAE

Novumbra hubbsi, USNM 357403, 2 specimens, 57.2–59.7 mm.

Plate 48

Description.

Remarks. In general the two dissected gill arches were very similar, but because of small size and fragility, both our dissections involved damage. The description and illustrations are mostly based on the larger specimen, but the posterior view is based on the smaller specimen.

LE1 on Eb1 uncinat process at and just ventrolateral to cartilaginous tip.

LE2 on Eb2 uncinat process at and, variably, just ventrolateral to cartilaginous tip.

LE3 on tip Eb3 uncinat process dorsoanteriorly.

LE4 weak, on Eb4 dorsoposteriorly near distal end, ventral fibers continuous with Ad4 dorsoposteriorly.

Remarks. Johnson and Patterson (1996:273) reported that *Novumbra* lacks LE4. The muscle is present in both of our specimens. Because LE4 is poorly developed and specimens are small, the muscle could have been easily lost during dissection.

LP absent.

LI1 dorsomedially on bony surface of Pb2.

LI2 on Pb3 dorsoposteriorly.

LI3 on Pb4 dorsolaterally meeting junction of Pb4 with UP4.

TD complex. Distinct TPb3a anteriorly, attaching to Pb3 uncinat process anteriorly, continuous pos-

teriorly by crisscrossing muscle bands (both specimens) with TPb3p. TPb3p irregular, attaching to dorsoposteromedial surface of Pb3, continuous posteriorly with TPb4 by continuations of crisscrossing muscle bands, which meet raphe with OD4' posteriorly. TPb4 attaching to Pb4, muscle continuous with SO posteriorly.

OD3–4 comprises a fused single muscle in the larger specimen (illustrated) and separate muscles (OD3 and OD4) in the smaller specimen. The fused muscle in the larger specimen can be artificially separated, with the OD3 portion much more slender than the OD4 portion (relative sizes not apparent in illustration). The fused muscle divides slightly at its insertions on Eb3 and Eb4, which are similar to the insertions of the two muscles in the smaller specimen. In the smaller specimen, the two muscles are of about equal size and are described as follows:

OD3 origin anteriorly on Pb3 dorsal surface ventral to TPb3a, insertion on medial edge of Eb3 uncinat process.

OD4 origin on Pb3 dorsal surface posterior to and continuous with OD3 origin, insertion on dorsomedial all bony process of Eb4, fuses with insertion of OD4'.

OD4' origin dorsally from raphe with crisscrossing muscle bands of TPb3p and mainly ventrally on dorsal surface of Pb4, insertion on dorsomedial bony process of Eb4, fuses with insertion of 4 portion of OD3–4.

Remarks. OD4' of *Novumbra* is similar to OD4' of the putatively related *Esox*, particularly in that both have their main origins on Pb4 rather than Pb3. There is also a similarity with OD4' of *Lepidoglossias* (Plate 41).

OP on mid-dorsoposterior margin of Eb4, ending ventrally at ER on Cb4 with Ad5.

M. Pb3–Eb3 small, attached to dorsoposterior edge of Pb3 uncinat process and dorsomedial edge of Eb3 uncinat process near LE3 insertion.

Ad1–3 absent, but GFM2 and 3 unusual, superficially like RecDs. GFM2 originates on dorsoanterior surface of Eb2 uncinat process and inserts on dorsoposterior edge of Eb1 uncinat process, where it is continuous with LE1 basally (not continuous basally with LE1 in smaller specimen). GFM3 (not illustrated) slender muscle seen only on right side of smaller specimen, originates on anterior margin of Eb3 and inserts on posterior surface of Eb2 uncinat process.

Remarks. Similar GFM2 and 3 are known among pre-acanthomorphs otherwise only in *Dallia* (Umbriidae), which has a modified GFM1. GFM1 in *Novumbra* was destroyed before it was realized that its character state might have importance.

Ad4 on Eb4 dorsoposteriorly and Cb4 dorsally just medial to Eb4–Cb4 joint, just meeting and joining ER at dorsodistalmost end of Ad5.

Ad5 on posterodistal surface of Cb4, joining ER with ventral end of OP, and on dorsoposterior portion of Cb5, forming raphe ventrally with TV5.

SO longitudinal muscle fibers begin well posterior to horizontal between posterior ends of Cb5s and extend anteriorly to below mid-posterior margin of TPb3a.

RDs absent.

Additional remarks. SCL attached mid-dorsally to posteroventrally extending cartilaginous end of Bb3. TV4 free from Cb5s. Eb4 uncinat process bony. UP5 absent. Eb5 absent.

Dallia pectoralis Bean, USNM 111643, 107 mm.

Not illustrated

Description.

LE1 on anterior surface of Eb1 uncinat process.

LE2 on anterior surface of Eb2 uncinat process.

LE3 dorsoanteriorly on Eb3 uncinat process.

LE4 mostly on Eb4 bony dorsolateral surface, extending onto cartilaginous distal end.

LP absent.

LI1 on dorsomedial bony surface of Pb2.

LI2 on Pb3 dorsally.

LI3 on Pb4 dorsally.

TD comprising TPb3 and TPb4. TPb3 shorter and wider of the two transverses, attaching to Pb3 dorsoanteriorolaterally; on left side attachment is dorsal to OD3 and OD4 origins; on right-side, posterolateral edge forms raphe with OD3 and OD4 origins and with slender muscle (anomalous?) extending laterally and inserting on Eb2 uncinat process; continuous broadly posteriorly with anterior end of TPb4. TPb4 on dorsal surface of Pb4 medial to LI3 insertion, continuous posteriorly with SO, but noticeably distinguished by change from horizontal (TPb4) to curving muscle fibers (SO).

OD3 origin on Pb3 (see TPb3 above), insertion on dorsomedial edge of Eb3 uncinat process.

OD4 origin on Pb3 (see TPb3 above), inserting laterally on Eb4 dorsomedial edge, extending medially along raphe with dorsal end of OP (left-side OD4 posterolaterally and OP dorsally forming free strap of muscle—not attached ventrally; right-side raphe almost completely attached to dorsal edge of Eb4).

OP dorsally joining raphe with OD4 (q.v.), ventrally on posterodistal end of Cb5, forming raphe (not ER, unless highly modified) posteroventrally with Ad5, posterolaterally overlapping Ad4 and apparently fusing with Ad4 (q.v.) ventroanteriorly on Cb5.

Ad1–3 absent, but GFM1–3 unusual; GFM2 and GFM3 RecD-like, similar condition observed only in *Novumbra*. GFM1 originates by long, slender tendon attaching to anterior surface of cartilaginous medial end of Eb1, becoming musculous in area anterior to

uncinat process, and covering (attaching to) most of dorsal surface of Eb1 lateral to distal end of Eb1, there becoming slenderer and extending around Eb1–Cb1 joint and continuing along dorsoanterior edge of Cb1. GFM2 inserts by short, fine tendon to posterior edge of Eb1 ventral to uncinat process, muscle is over CT between Eb1 and Eb2 and attaches to anterior edge of Eb2. GFM3 similar to GFM2, insertion on Eb2 and origin on Eb2.

Ad4 dorsally broadly on Eb4 beginning anterior to lateral end of OP and extending to end of bone; anteroventrally on Cb4 dorsal surface medial to Eb4–Cb4 joint; posteroventrally attaching to cartilaginous finger-like process extending medially from posterodistal end of Cb4, there joining raphe with Ad5, and continuing ventrally and (unusually) attaching to Cb5 anterior to OP, with which it appears to fuse.

Ad5 very short, joins dorsodistal end of Cb5 to posterodistal end of Cb4, joins raphes with OP and Ad4.

SO beginning well posterior to horizontal through posterior ends of Eb4s and extending anteriorly to posterior margin of TPb3.

RDs absent.

Additional remarks. SCL interrupted mid-posteriorly by attachment to posteroventrally extending cartilaginous end of Bb3. TV4 attached to Cb5s, except for free short area at anterior end of muscle. UP5 absent. Eb5 absent.

Umbra pygmaea (DeKay), USNM 343617, 61.1 mm.

Plate 49

Description.

LE1 on Eb1 uncinat process.

LE2 on Eb2 uncinat process.

LE3 on Eb3 uncinat process; right side LE3 with muscle slip inserting on anteromedial edge of Eb4.

LE4 on cartilaginous dorsodistalmost edge of LE4.

LP absent.

LI1 on Pb2 dorsoposteromedially.

LI2 on Pb3 bony dorsal surface; posterior edge continuous with anterior edge of LI3, but slight break at anteroventralmost insertion of LI3 on Pb4.

LI3 on Pb4 dorsally (see also LI2).

TD comprises single continuous sheet of muscle, TPb3–Pb4–Eb4, continuous posteriorly with SO.

OD3 origin on Pb3 anterodorsal surface continuous with OD4 origin, insertion on medial edge of Eb3 uncinat process ventral to OD4.

OD4 origin on Pb3 anterodorsal surface immediately at and posterior to OD3 origin, forming raphe medially with TPb3–Pb4–Eb4, insertion on dorso-medial edge of Eb4 at and just anterior to dorsal attachments of Ad4 and OP.

OP separate band of muscle dorsally, attaching to

dorsomedial edge of Eb4 just medial to dorsal attachment of Ad4, just posterior to OD4 insertion, and partially overlying (posterior to) SO attachment to posterior surface of Eb4; joins ER ventrally at about mid-level of cartilaginous Eb5, below which OP is inseparable from SO.

Ad1–3 absent (condition of GFM not determined).

Ad4 dorsally on dorsoposterior edge of Eb4 ventral to LE4 insertion and lateral to OP attachment, ventrally on Cb4 at and medial to inner angle formed by Eb4-Cb4.

Ad5 on distal surface of Eb5 and dorsodistalmost end of Cb5.

SO longitudinal muscle fibers begin well posterior to horizontal at posterior ends of Cb4s and extend anteriorly only to horizontal between mid-length of Pb4s.

RD absent.

Additional remarks. SCL attached mid-posteriorly to ventral surface of cartilaginous posterior end of Bb3. TV4 questionably absent (rare condition), but an obliquus ventralis-like muscle attaches ventromedial surface of each Cb4 to ventral surface of Bb4 cartilage. UP5 absent. Eb5 present.

Stomiiformes

DIPLOPHIDAE

Diplophos taenia Günther, USNM 206614, 190 mm.

Plate 50

Description.

LE1 very fine, on small bony process on lateral margin of Eb1 uncinat process.

LE2 very fine, on small bony process ventrolateral to expanded cartilaginous dorsomedial end of Eb2.

LE3 slender, on dorsomedial bony edge of Eb3 uncinat process on and with OD3 insertion.

LE4 originates in cluster with other LEs; inserts tendinously on dorsal tip of Eb4 levator process.

LP absent.

LI1 on most of length of dorsomedial edge of Pb2.

LI2 dorsally on posterolateral edge of Pb3.

LI3 on dorsolateral edge of UP5, meeting TUP5 laterally.

Remarks. A slight portion of the posterior end of UP5 slips under the medial end of Eb4. We follow Johnson (1992) in recognizing the single tooth plate in stomiiforms as UP5. However, its close association with Pb4 suggests that it could be UP4. Further investigation of the homology of this tooth plate is desirable.

TD comprises TEb2, TEb2v, TPb3, and TUP5. TEb2 broadest, on Eb2 dorsoanteriorly, attaching to expanded cartilaginous medial end of Eb2 as muscle passes over it, continuous posteriorly by diagonal

strand of muscle with TPb3. TEb2v thin muscle tightly attached to CT covering anterior ends of Pb3s, lies anteroventral to TEb2, with thin, slender posterolaterally extending straps that attach to antero-medial surface of expanded cartilaginous medial end of Eb2 (verification of presence in other specimens desirable). TPb3 attaches dorsally on posterolateral edge of Pb3 with and medial to LI2 insertion, continuous posteriorly by diagonal strand of muscle with TUP5. TUP5 attaches to UP5 anteromedial to LI3 insertion, is continuous posteriorly by diagonal strand of muscle with SOD.

OD3 origin ventral to TEb2 beginning on Pb3 dorsally a short distance posterior to anterior cartilaginous tip of Pb3 and continuing uninterrupted posteriorly as OD4 origin to point a little posterior to beginning of cartilaginous posterior end of Pb3; OD3 separates dorsolaterally from OD4 shortly posterior to combined origins and inserts on Eb3 uncinat process anteriorly.

OD4 origin on Pb3 continuous with OD3 origin, joins OD4' posterolaterally, and insert together on anterior surface of Eb4 levator process.

OD4' originates on Pb4 anteriorly, beginning at edge joining Pb3, joins OD4 posteromedially, and together insert on Eb4 levator process anteriorly.

OP dorsally on Eb4 posteroventrally beginning near medial end and extending laterally a short distance, ventrally on Cb5 slightly posteromedial to distal end; ER absent.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly beginning laterally at Eb4 levator process and extending medially about half distance to medial end of bone; ventrally narrowly on Cb4 dorsoposteriorly medial to inner angle formed by Eb4-Cb4 joint; medial edge of muscle tendinous.

Ad5 dorsally on Eb4 dorsodistally, ventrally on Eb5 (not illustrated) and posterodistally on Cb5, joining raphe with TV5.

Remarks. Ad5 completely occludes the tiny Eb5 from view. Fink and Weitzman (1982), using single stained material, did not report the existence of Eb5 in *Diplophos taenia* (their fig. 10 is based on a specimen from the same lot as ours). Baldwin and Johnson (1996:372), using double-stained material, reported that Eb5 is present in *Diplophos taenia*.

RDs separate by space equal to about diameter of one RD, muscle inserts on dorsomedial edge of UP5 at junction with Pb4.

SO longitudinal muscle fibers questionably present; requires histological examination.

SOD present.

Additional remarks. SCL absent. TV4 free from Cb5s. Identity of single UP questionable (see remarks following LI3).

STERNOPTYCHIDAE

Maurolicus muelleri (Gmelin), USNM 323033, 2 specimens, 54.7–55.7 mm.

Plate 51

Description.

Remarks. The muscles are thin and tiny and it is possible that alternative descriptions we provide in remarks following LE3, LE4, and OD4 may apply.

LE1 very fine, inserts by extremely fine tendon on mid-dorsoposterior edge of Eb1 lateral to uncinat process.

LE2 very fine, inserts by extremely fine tendon on mid-dorsoposterior edge of Eb2.

LE3 on tip of Eb3 uncinat process.

Remarks. Possibly comprising a bilateral pair of closely applied muscles (LE3, LE3'), based on what appears to be a divided origin (attempts to separate muscle into two natural parts were inconclusive).

LE4 originates with cluster of other LEs; inserts on tip of Eb4 levator process.

Remarks. Possibly comprising a bilateral pair of closely applied muscles (LE4, LE4'), based on what appears to be a divided origin (attempts to separate muscle into two natural parts were inconclusive).

LP absent.

LI1 on Pb2 dorsomedial surface posterior to uncinat process.

LI2 on dorsoposterior surface of Pb3.

LI3 on UP5 dorsally at junction with cartilaginous Pb4.

Remarks. Johnson (1992:fig. 3c) illustrated the upper pharyngeal bones of *Maurolicus* and the insertions of LI1–3 and RD. See also remarks regarding UP5 following LI3 in *Diplophos*, Diplophidae.

TD comprises TEb2a, TEb2p, and TPb3–Pb4 (larger specimen) or TPb4 (smaller specimen). TEb2a overlies bony anterior ends of Pb3 and attaches anteriorly on dorsomedial surface of Eb2, separated from TEb2p by depression. TEb2p on dorsoposterior surface of Eb2, extending slightly further distally than TEb2a, overlies OD4 origins. TPb3–Pb4 slightly posteroventral and unconnected to TEb2p, attaches to dorsomedial edges of Pb3 and Pb4 and is indistinguishable posteriorly from SOD; TPb4 is separated from TEb2p by a relatively large gap in smaller specimen.

Remarks. Separation of TEb2 into TEb2a and TEb2p is problematic.

OD3 absent.

Remarks. Absence of an OD attachment to Eb3, either as OD3 or OD3–4, is an uncommon specialization within the Euteleostei, and occurs only in some Stomiiformes (Table 1) and ateleopodids. It may contribute to resolution of the Neoteleostei trichotomy (Fig. 3).

OD4–4' origin ventral to TEb2p, on most of dor-

soposterior surface of Pb3 and all of dorsal surface on Pb4, insertion broadly on dorsolateral surface of Eb4 levator process.

Remarks. There is a definite separation of the origins on Pb3 and Pb4 in the larger specimen, but little or none in the smaller specimen. OD4', originating on Pb4, is present in other stomiiforms we examined, and we infer that OD in *Maurolicus* represents a fusion of OD4 and OD4'.

OP absent, ER absent.

Ad1–3 absent.

Ad4 dorsally broadly on posterodorsal surface of Eb4 ventral to LE4, ventrally narrowly on Cb4 dorsal surface just medial to inner angle formed by to Eb4–Cb4 joint.

Ad5 dorsally on posterodistal end of Eb4, ventrally on dorsodistal surface of Cb5, joining raphe with TV5 (not illustrated) ventroanteriorly in smaller specimen, but not in larger specimen.

RDs separated by distance greater than one RD, on UP5 at junction with Pb4 (see remarks under LI3).

SO longitudinal muscle fibers questionably present, requires histological verification.

SOD present, but broadly continuous with TPb3–Pb4 anteriorly.

Additional remarks. SCL absent. TV4 free from Cb5s. Identity of single UP questionable.

GONOSTOMATIDAE

Gonostoma elongatum Günther, USNM 330309, 162 mm.

Plates 52.1, 52.2

Description.

LE1 very fine, inserts by long thread-like tendon to dorsal edge of Eb1 lateral to base of uncinat process.

LE2 absent.

Remarks. Absence of LE2 rare in fishes.

LE3 slender, inserts by very long tendon to cartilaginous tip of Eb3 uncinat process.

LE4 relatively large, originates in cluster with other LEs, inserts by tendon on dorsomedial cartilaginous end of Eb4 levator process.

LP absent.

LI1 massive, on almost entire medial edge of Pb2, lateral edge joins or is formed by tendon, which inserts on Eb1 uncinat process.

LI2 on posterolateral edge of Pb3.

LI3 on lateral surface of UP5.

Remarks. See also remarks regarding UP5 following LI3 in *Diplophos*, Diplophidae.

TD comprises TEb2 anteriorly and well separated TUP5 posteriorly. TEb2 attaches broadly on Eb2 anteromedially, giving rise dorsoanteriorly on each side to short muscle lamina that attaches to tendon inserting on Eb1 uncinat process, joins raphe with

OD4 origin beginning at tendon and extending entire length of OD4 origin. TUP5 a small muscle strap attaching to lateralmost edge of UP5.

OD3 absent (see remarks under OD3 in *Maurollicus*, Sternoptychidae).

OD4 originating dorsally at raphe with TEb2 and ventrally on Pb3 dorsal surface, inserting on anterior surface of Eb4 levator process.

Remarks. Left-side OD4 appears to have two almost continuous origins, and the muscle divides at about mid-length with the ventral branch attaching separately to Eb4 ventral to OD4'.

OD4' originating on dorsal surface of Pb4 and inserting on medial edge of Eb4 levator process.

M. UP5-Cb4 of left side originating by long tendon on medial edge of UP5 close to Pb4-Eb4 joint and inserting by long tendon on posterodistalmost cartilaginous surface of Cb4 close to tiny sesamoid bone (not illustrated) on medial side of Eb4-Cb4 joint; muscle on right side originating as pair of slender tendons, one on medial edge of UP5 close to Pb4-Eb4 joint and the other on ventromedialmost bony edge of Eb4, tendons uniting just before inserting as on left side.

Remarks. The tiny sesamoid bone was not seen on either side of two cleared and stained specimens, ca. 130 mm (USNM 327091).

OP dorsally on ventral surface of thick medial arm of Eb4, ventrally at and medial to Ad5 insertion on Cb5, interrupted by ER at about mid-length, but clearly continuous ventral to ER.

Remarks. Other than *Gonostoma*, the dorsal attachment of OP is always on the dorsoposterior surface or posteroventral edge of Eb4.

Ad1-3 absent.

Ad4 broadly on dorsoposterior edge of Eb4 levator process, narrowing almost to point at tendinous insertion on posteromedial end of Cb4.

Ad5 on Eb4 near dorsodistal end and Cb5 dorso-distal end; ligament runs along lateral edge of Ad5.

RDs appressed medially, insert on posteroventromedial surface of UP5.

SO longitudinal fibers appear to begin at about horizontal joining Eb4 uncinat processes and end anteriorly at attachments to medial surfaces of UP5s.

SOD a thin strap arising from SO and medial edge of ER and extending dorsoanteriorly along dorsoposterior surface of Eb4 from one side to other.

Additional remarks. SCL absent. TV4 free from Cb5s. Identity of single UP questionable.

Ateleopodiformes

ATELEOPODIDAE

Ateleopus loppei (Roule), USNM 349721, ca. 350 mm TL, Eastern Atlantic.

Plate 53

Additional material. ② = *Ateleopus* sp., USNM 359636, ca. 300 mm TL, Caribbean, only partial left-side dorsal gill arches (information provided for all muscles for which information is ascertainable). ③ = Ateleopodidae, USNM 361124, Vityaz Cruise station 2560, W. Indian Ocean, small specimen, only incomplete left-side dorsal gill arches (information provided below for all muscles for which information is ascertainable).

Description.

LE1 on Eb1 posterodorsal surface distally, comprises two separate elements oriented longitudinally on each side, right-side with additional element medial to paired elements. ③ Comprises single element on each side.

LE2 on Eb2 posterodorsal surface distally. ③ Same.

LE3 slender, on connective tissue between Eb3 and Eb4 distally. ③ Same.

LE4 on Eb4 dorsodistally. ③ Same.

LP absent. ③ Same.

LI1 on Pb2 dorsally. ② Same.

LI2 on Pb3 bony surface dorsally, fuses dorsally with LI3 ventral to origin. ③ Same.

LI3 left side: on cartilaginous posterior end of Pb3 laterally, fuses dorsally with LI2 ventral to origin; right side: on bony and cartilaginous posterior end of Pb3 laterally, fuses dorsally with LI2 ventral to origin. ② ③ on Pb3 bony surface dorsoposteriorly and anterolateral surface of UP5, fuses dorsally with LI2 ventral to origin.

Remarks. Johnson (1992:11), who did not examine ateleopodids, stated that LI3 inserts on Pb4 in all non-neotelosts but among neoteleosts, shifts its insertion to UP5 in stomiiforms and aulopiforms; LI3 and UP5 are absent in ctenosquamates.

Olney et al. (1993:154), based on a specimen of *Ateleopus japonicus* Bleeker, reported that LI2 inserts on Pb3 and LI3 inserts on UP5. Ateleopodids lack Pb4, and so the insertion of LI3 would be expected to occur on one or both, Pb3 and UP5. Whether the insertion of LI3 on some portion of Pb3 in USNM 349721 is typical or atypical for that species, does not bear on the problematic phylogenetic position of ateleopodids.

TD comprises TEb2 and TPb3. TEb2 attaches to Eb2 dorsoposterior margin and is posteriorly continuous with TPb3, which attaches to Pb3 dorsomedial margin and is continuous posteriorly with SO. ③ Same.

OD3 absent. ③ Same.

OD4 origin on Pb3 dorsally near anteriormost tip, insertion on Eb4 dorsal bony surface just medial to LE4 insertion. ② Same.

Remarks. Absence of Pb4 in ateleopodids presents difficulties in inferring synapomorphic states for the

origin of OD4. See synapomorphies (34) (35) in Results section.

OP distinct dorsally as fan of muscle inserting on Eb4 posteromedially, extending ventrally and fusing with SO medially, becoming continuous ventrolaterally with AD5 at posteriormost ventromedial edge of Cb4, where both attach to Cb4 by CT. ER absent.

Ad1–3 absent.

Ad4 posteroventrally on Eb4 lateral to OP (not visible in dorsal view), ventrally on dorsodistal cartilaginous end of Cb4 just medial to Eb4–Cb4 joint.

Ad5 dorsolaterally on posteromedialmost end of Cb4, ventrally on posterolateral end of Cb5, medially inseparable from OP (see OP above).

RD broad, thick, dorsomedian sheet completely included in SO, divides anteriorly at horizontal joining Eb4s at mid-length, attaches to UP5 and almost entire medial surface of Pb3.

SO longitudinal fibers very sparse, restricted to ventralmost area of SO.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 absent.

Aulopiformes

AULOPIDAE

Aulopus filamentosus (Bloch), USNM 313689, 167 mm.

Plate 54

Description.

LE1 on lateral edge of Eb1uncinate process.

LE2 on anterior surface of lateral end of uncinate process at and lateral to insertion of TEb2.

LE3 on cartilaginous tip of Eb3 uncinate process just dorsal to OD3 insertion.

LE4 origin clusters with other LEs; insertion on dorsal bony surface of Eb4 posterolaterally.

LP absent.

LI1 on Pb2 dorsally at and medial to base of uncinate process.

LI2 on posterodorsal surface of Pb3 at and lateral to TPb3' attachment and on Pb4 at and lateral to TPb4 attachment anteriorly.

LI3 on dorsoanterior surface of UP5, anteriorly at and lateral to mid-point of attachment of TPb4 to Pb4.

Remarks. Nelson (1967a:286) stated mistakenly that *Aulopus* has only two LIs. Johnson (1992) argued persuasively that LI3 in Neoteleostei has shifted its insertion from Pb4 to UP5. He illustrates his interpretation in his fig. 3b of *Aulopus*.

TD comprises TPb2–Pb3a, TEb2, TPb3p, TPb3', TPb4, and TEb4. TPb2–Pb3a anteriorly on dorso-medial surface of Pb2 anterior to LI1, continuing on dorsomedial surface of anterior portion of Pb3 anterior to OD3 origin, continuous posteriorly with TEb2

by diagonal muscle strand. TEb2 on most of anterior surface of Eb2 uncinate process, ending laterally at medial edge of LE2 insertion, partially dorsal to OD3 origin and anterolateral portion of TPb3p, continuous mid-posteriorly with TPb3p. TPb3p on Pb3 mid-dorsolaterally anterior to LI2 insertion, weakly continuous mid-posteriorly with TPb3'. TPb3' on Pb3 posterolaterally just medial to LI2 insertion, well-separated laterally, but broadly continuous mid-posteriorly with, TPb4. TPb4 on Pb4 posterolaterally, abutting TEb4 mid-posteriorly. TEb4 attaching to Eb4 posteromedially dorsal to SO and, on left side only, ventral to dorsomedial OP fibers, posteriorly abutting SO.

Remarks. The various divisions of TD are fairly well differentiated and more numerous than in any other taxon we examined.

OD3 origin on Pb3 ventral to TEb2, insertion on dorsolateral surface of Eb3 uncinate process.

OD4 origin on Pb3 ventral to TPb3p, insertion on dorsomedial edge of Eb4 uncinate process.

LP absent.

OP dorsally on dorsoposterior edge of Eb4 including uncinate process, joining raphe dorsally with OD4 insertion, ventrally joining ER at ventroposterior end of Eb5; not distinguishable from SO or Ad5 below ER.

Ad1–3 absent.

Ad4 dorsally on dorsoposterior edge of Eb4, ventrally broadly on Cb4 dorsal surface medial to inner angle formed by Eb4–Cb4 joint.

Ad5 dorsally on distal end of Eb5 and slightly on distal end of Cb4, ventrally on Cb5 posterodistally, dorsomedially joining raphe with OP, medially not separable from OP.

RD not represented externally, comprises, single, broad, thick bundle of longitudinal fibers dorsally in esophagous between outer transverse SO muscle and inner mucosal layer; divides anteriorly at about level of medial end of Eb3, inserts on medial edge of Pb4 and UP5 and along medial edge of posterior half of Pb3.

Remarks. Nelson (1967a:286) noted that paired RDs in *Aulopus* are absent, and described the insertion of this muscle as follows: “. . . fibers anteriorly attach mostly to the connective tissue of the pharyngeal roof . . .”

SO longitudinal fibers questionably present; histological verification needed (see remarks following RD under *Saurida*).

Additional remarks. SCL present, attached anteriorly to ventromedialmost end of Hb3, with ligament arising dorsally from mid-posterior edge and attaching to ventroanterior surface of Bb3. TV4 free from Cb5s.

SYNODONTIDAE

Saurida gracilis (Quoy and Gaimard), USNM 140822, 131 mm.

Plate 55

Description.

LE1 on tip of Eb1 uncinat process.

LE2 on Eb2 just lateral to distal end of uncinat process and at and anterior to lateralmost attachment of TEb2.

LE3 on tip of Eb3 uncinat process.

LE4 on Eb4 amid OD4 insertion; origin clustered with other LEs.

LP absent.

LI1 broadly on Pb2 anterior process just lateral to TPb2 attachment.

LI2 on Pb3 posterolaterally.

LI3 on posterolateral surface of UP5.

Remarks. See remarks following LI3 in account of *Aulopus filamentosus*.

TD comprises TPb2, TEb2, TEb3, and TEb4. TPb2 on Pb2 medial to LI1 insertion, dorsal to M. Pb2-Eb2 origin, continuous posteriorly by diagonal muscle strap with TEb2. TEb2 on anterior bony surface of Eb2 uncinat process, continuous posteriorly by diagonal muscle strap with TEb3. TEb3 on dorsoposterior surface of medial end of Eb3 ventral to OD3 insertion and OD4; posteriorly, TEb3 abuts fibers of TEb4. TEb4 slender muscle band on mid-dorsoposterior surface of Eb4, attachment ventral to dorsal end of OP, posteriorly abuts fibers of SO.

M. Pb2-Eb2 slender, longitudinal muscle, anteriorly on Pb2 ventromedial to TPb2 attachment, posteriorly on anterior edge of medial end of Eb2 uncinat process partially coincident with TEb2 attachment.

OD3 origin broadly on Pb3 dorsomedially ventral to TPb2 and anterior to OD4 origin, extending posteriorly ventral to TEb2 and inserting on anterior and posterior surfaces of Eb3 uncinat process.

OD4 origin on Pb3 posteromedial to posterior end of OD3 origin, insertion on anterior and posterior surfaces of dorsal crest of Eb4.

OP broad, on Eb4 dorsoposterior edge medial to dorsal attachment of Ad4 and ventral to TEb4, ventrolaterally joins—ends at—ER at level of distal end of Eb4, fuses with SO ventromedially.

Ad1–3 absent.

Ad4 dorsally on lateral dorsoposterior edge of Eb4, ventrally on Cb4 dorsal surface medial to inner angle formed by Eb4-Cb4 joint.

Ad5 dorsally on posterodistal end of Cb4, ventrally on posterodistal end of Cb5, ventromedially joins raphe with TV5, dorsally joins ER with OP.

RD not represented external to SO, comprises bilateral pair of larger, longitudinal muscle bundles ventrally (RD) and very weakly differentiated small-

er pair dorsally (RD'); RD' fibers divide at posterior end of Pb3s and each division extends anteriorly, inserting along medial edge of most of posterior half of Pb3; RD fibers attach to UP5.

Remarks. Large longitudinal muscle bundle present on each side ventrally in esophagus between transverse muscle and mucosal layers (ventral muscle bundle absent in *Aulopus*). There are no longitudinal muscles in the lateral walls of the esophagus.

Additional remarks. SCL absent. TV4 free from Cb5s. UP4 and Eb5 absent.

CHLOROPHTHALMIDAE

Chlorophthalmus agassizi Bonaparte, USNM 357798, 121 mm, USNM 159379, 2 specimens, 119–125 mm.

Plate 56

Description.

LE1 dorsolaterally on bony edge of Eb1 uncinat process just ventral to tip.

LE2 on dorsolateralmost surface of distal end of Eb2 uncinat process.

LE3 dorsoanteriorly on tip of Eb3 uncinat process.

LE4 on dorsal tip of Eb4 levator process.

LP absent.

LI1 on bony anterior edge of Pb2 uncinat process.

LI2 on dorsoposterior surface of Pb3.

LI3 anterior third on Pb4 lateral surface, posterior two-thirds on dorsoanterior edge of UP5 at junction with Eb4.

TD comprises TPb2-Pb3a, TEb2, TPb3p-Pb4, and TEb4. TPb2-Pb3a laterally on medial ends of proximal Pb2 uncinat process, attaching ventromedially to Pb3 dorsoanterior surface, continuous posteriorly by diagonal muscle strand with TEb2. TEb2 very slender, on dorsomedial surface of proximal end of Eb2 uncinat process, posteriorly continuous by diagonal muscle strand with TPb3p-Pb4. TPb3p-Pb4 on dorsomedial surfaces of Pb3 and Pb4, continuous posteriorly with TEb4. TEb4 on dorsomedial end of Eb4, continuous posteriorly with SO.

OD3 origin on Pb3 just posteroventral to TEb2 and at and dorsal to posterior portion of OD4 origin, laterally dorsal to OD4 for much of length of OD4; insertion on Eb3 uncinat process just ventral to LE3 insertion.

OD4 origin on Pb3 anteriorly ventral to TPb2-Pb3a and TEb2 and posteriorly on Pb4 anterodorsal surface ventral to OD3, laterally ventral to OD3 for much of length of OD4; insertion broadly on bony anterior surface of Eb4 levator process.

OP one or two straps of muscle attaching dorsally to Eb4 dorsoposterior edge just medial to dorsal attachment of Ad4, and ventrally to Cb5 posterior sur-

face medial to Ad5 attachment, only slightly differentiated medially from SO. ER absent.

Ad1–3 absent.

Ad4 broadly dorsally on Eb4 dorsoposterior edge lateral to OP attachment, ventrally on Cb4 dorsal surface just medial to inner angle formed by Eb4–Cb4 joint.

Ad5 dorsally on posterodistal ends of Cb4 and Eb5, ventrally on posterodistal surface of Cb5.

RD origin tendinous, muscle undivided (unpaired), completely ventral to SO transverse muscle layer, extending broadly anteriorly and becoming continuous with ventral surface muscle fibers of TPb2–Pb3a, attaching to Pb3, Pb4, and Eb4.

SO longitudinal muscle fibers questionably present; need histological verification.

Additional remarks. SCL absent. TV4 free from anterior ends of Cb5s.

Myctophiformes

NEOSCOPELIDAE

Neoscopelus macrolepidotus Johnson, USNM 358034, 127 mm; TCWC 7012.06, ca. 76 mm.

Plate 57

Description.

Remarks. The description is based on both specimens, but the illustration is based on the larger specimen because the smaller specimen was deeply dissected before it was decided to illustrate the taxon. The muscles in the larger specimen are more robust and folded than in the smaller specimen, and some elements (e.g., ER) and attachments are not readily visible without removing folds of overlying muscle, whereas in the smaller specimen the elements are more obvious.

LE1 very weak, on mid-dorsoposterior edge of Eb1 well lateral to uncinat process.

LE2 on raised dorsoposterior edge of Eb2 somewhat lateral to mid-length (uncinat process absent).

LE3 on anterior edge of Eb3 uncinat process posterior to OD3 insertion, extends anteriorly medial to LI2.

Remarks. In the smaller specimen, the uncinat process of Eb3 and levator process of Eb4 are tightly bound together. In the larger specimen, they are separated as illustrated, but thin, strong tendinous connective tissue joins the processes and muscles that the tissue passes over.

LE4 on Eb4 levator process just proximal to cartilaginous tip, surrounded anteriorly by OD4 insertion, extends anteriorly medial to LI2.

LP absent.

LI1 on Pb2 medial to uncinat process and somewhat ventral to TPb2a, passes medial to LI2.

LI2 on Pb3 dorsolaterally just anterior to joint with medial end of Eb3.

LI3 absent.

Remarks. Johnson (1992) argued persuasively that the concomitant loss of LI3 and UP5 are a synapomorphy of Ctenosquamates.

TD complex, comprises TPb2a, TPb2p, TEb2, TPb3, and TEb4. TPb2a dorsally on Pb2 between dorsoanteriorly projecting cartilaginous end and cartilaginous tip of uncinat process, noticeably separate from TPb2p laterally and dorsally, but continuous posteroventrally with it. TPb2p on dorsal bony surface of Pb2 just medial to LI1 insertion, continuous posteriorly with TEb2. TEb2 on Eb2 dorsomedially, near articulation with Pb3, continuous posteroventrally with TPb3. TPb3 extensive longitudinally, lies dorsal to Pb3s, muscle strands extending ventrally from mid-anteroventral surface (ventral to TEb2) attach to medial surfaces of Pb3s, joins raphe laterally on each side with origins of OD3 and OD4, posteroventrally continuous with TEb4. TEb4 on Eb4 between OD4 insertion and OP dorsal attachment.

OD3 origin on Pb3 laterally ventral to TPb2p and TEb2, joins raphe anteriorly with TPb3, continuous with OD4 origin (fibers appear separate dorsally but mesh ventrally), separating from OD4 posterolaterally before inserting on Eb3 uncinat process anteroventral to LE3 insertion.

OD4 origin from dorsal raphe with TPb3 and dorsomedial surface of Pb3, insertion on Eb4 levator process.

OP dorsally on Eb4 uncinat process medial to Ad4 attachment and ventral to OD4 insertion, interrupted by ER at mid-length (ER extends tendinously laterally and attaches to Cb4 distally together with dorsal end of Ad5), but continues below ER and joins raphe with anteroventral portion of Ad5 and lateral end of TV5 before attaching to Cb5 medial to raphe.

Ad1–3 absent.

Ad4 dorsally on Eb4 posterolateral edge lateral to OP, ventrally on Cb4 medial to inner angle formed by Eb4–Cb4 joint.

Ad5 on Cb4 distal end at attachment of ER lateral tendinous extension, joins raphe with Ad4 anteroventrally and TV5 medially.

RD large muscle cluster consisting of dorsal, incompletely separated bilateral pair of bundles with ventral, somewhat triangular, incompletely separated bundle (RD') between them, inserting on posterior surface of Pb3 and Pb4 and posterior edge of UP4, and extending anteriorly between and attaching to medial surfaces of Pb3s.

SOD ventral to TEb4.

SO longitudinal muscles restricted to dorsal and ventral areas of SO.

Additional remarks. SCL absent. TV4 free from

Cb5s. UP5 and Eb5 absent. Eb4 uncinat process absent.

MYCTOPHIDAE

Lampanyctus macdonaldi (Goode and Bean), USNM 303167, 118 mm.

Plate 58A, B

Description.

LE1 absent, possibly represented by tough CT inserting on Eb1 uncinat process and attaching to skull (see remarks following LE1 in *Diaphus*).

LE2 on bony Eb2 process.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 origin tendinous; insertion on cartilaginous tip of Eb4 levator process coincident with OD4 insertion. Originates with tendinous origins of other LEs.

LP absent.

LI1a on Pb2 anterior to uncinat process (see remarks under LI1p).

LI1p on ventromedial surface of Pb2 uncinat process, questionably impinging on ventroposteriormost edge of LI1a insertion.

Remarks. LI1a and LI1p are more accurately described, perhaps, as separated by the posterolateral portion of TPb2a, which lies dorsal to the insertion of LI1p, rather than by the ascending process (= our uncinat process) of Pb2, as stated by Stiassny (1996: 407). Stiassny possibly based her remark on Johnson's (1992:fig. 7B) illustration of the condition in the myctophid *Diaphus mollis* (but see remarks under LI1a in our description of *Diaphus mollis*).

LI2 on posterolateralmost dorsal surface of Pb3.

LI3 absent.

TD comprises TPb2a, TPb2p, TEb2, TPb3, and TEb4. TPb2a on dorsal bony surface of Pb2 anterior to Pb2 uncinat process; muscle narrowly continuous posteromedianly with TPb2p. TPb2p on posterior arm of Pb2 dorsally, continuous posteriorly by diagonal muscle strand with TEb2. TEb2 on dorsal surface of medialmost end of Eb2 near articulation with Pb3. TPb3, separated by large gap from TEb2, which continues onto TEb4; muscle attached to Pb3 laterally ventral to OD3 and OD4, continuous posteromedianly with TEb4. TEb4 on mid-posterior surface of Eb4 ventral to OD4 insertion and medial to OP dorsal attachment, continuous mid-posteriorly with SOD.

Remarks. A median longitudinal raphe extends from the posterior half of TPb2p to posterior margin of TEb2, and another extends from TPb3 to dorso-posterior margin of SOD.

OD3 lies dorsal to mid-section of OD4; origin on Pb3 dorsomedial edge dorsal to, and coincident with, origin of OD4 mid-section; insertion dorsoanteriorly on Eb3 uncinat process ventral to LE3 insertion.

OD4 origin extensive, beginning on Pb3 dorso-

medial edge dorsal to TPb3 and continuing posteriorly ventral to OD3 origin, then dorsally to end of Pb3; insertion massive, on anterior surface of Eb4 levator process.

OP dorsally on Eb4 posterior surface medial to Ad4 dorsal attachment, interrupted by ER ventrally, but continuing and attaching to Cb5 just anterior to combined attachment of Ad5 and TV5 to Cb5.

Ad1–3 absent.

Ad4 dorsally on posterolateral surface of Eb4; ventrally, narrowly on Cb4 just medial to inner angle formed by Eb4–Cb4 joint.

Ad5 broadly on Eb4 posterolaterally and Cb5 dorsodistally, joining raphe with TV5 on Cb5.

RD on each side comprising large RD ventrally and small RD'. RD inserts completely separately from RD', attaching to posterior end of Pb4 and UP4 and medial end of Eb4; RD' joins longitudinal SO muscle layer at dorsoposterior end of Pb3 as layer divides bilaterally (similar to *Diaphus*, Plate 58C).

SOD present.

SO longitudinal muscle layer restricted to dorsal and ventral areas; dorsal section divides bilaterally at posterior end of Pb3s, each division extending anteriorly between Pb3s and attaching to anteromedial surface of its respective Pb3.

Additional remarks. SCL absent. TV4 free from Cb5s. UP5 and Eb5 absent. Eb4 uncinat process absent.

Jollie (1954) described and illustrated the gill-arch muscles of *Lampanyctus leucopsarus* (= *Stenobrachias leucopsarus* Eigenmann and Eigenmann), which are very similar to those of *L. macdonaldi*.

Diaphus mollis Tåning, USNM 300877 (Gulf of Mexico), 2 specimens, 50.5–54.4 mm; USNM 274201, 54.2 mm (E. of New Zealand).

Plate 58C

Description.

Remarks. We found no differences worth noting among the specimens of *D. mollis* from the two geographic areas.

LE1 very fine, on dorsal tip of bony process just lateral to tip of Eb1 uncinat process, where it is joined by insertion of medial edge of LE2.

Remarks. Stiassny (1996:412) stated that reduction of LE1 to a thin slip (Neoscopelidae) or ligament (Myctophidae) is a synapomorphy of myctophiform fishes. We agree that a reduced LE1 may be synapomorphic for myctophiforms, but we find that LE1 in myctophids also may be present as a thin slip of muscle.

LE2 on posterodorsal edge of Eb2 where bone widens; muscle extends anteriorly and attaches to

bony process on Eb1 lateral to uncinat process, thence continuing to origin on cranium.

LE2' very fine, becoming even finer and tendinous before inserting among LE2 fibers (absent in *Lampanyctus*).

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 on cartilaginous tip of Eb4 levator process coincident with Od4 insertion.

LI1 with single insertion equivalent to LI1a of *Lampanyctus macdonaldi*.

Remarks. Johnson (1992:fig. 1B) illustrated LI1 in a specimen putatively identified as *Diaphus mollis* (AMNH 29449). In contrast to our finding for the species, his figure shows LI1 as having anterior and posterior sections with insertions equivalent to LI1a and LI1p of *Lampanyctus macdonaldi* (q.v.). The specimen Johnson illustrated is actually identifiable as *D. dumerilii* (USNM 301132). AMNH 29449, however, is identifiable as *D. mollis* (from off Bermuda). M. Stiassny examined a specimen from the same AMNH lot and informed us (E-mail, 15 May 2000) that LI1 has a single insertion. Aside from *D. dumerilii* and *L. macdonaldi*, we find LI1 also has two insertions in *D. lucidus* (USNM 269439), *D. regani* (USNM 269381), *Hygophum hygomi* (USNM 206616), and *Protomyctophum normani* (USNM 206631). Stiassny (1996:407) interpreted the subdivision of LI1 as a synapomorphy of the Myctophidae. The character state for LI1 in *D. mollis* is probably autapomorphic.

LI2 on posterolateralmost dorsal surface of Pb3.

LI3 absent.

TD comprises TPb2a, TPb2p, TEb2, TPb3, and TEb4. TPb2a on dorsal bony surface of Pb2 anterior to Pb2 uncinat process, dorsal to anteriormost edge of LI1a insertion, and narrowly continuous postero-medially with TPb2p. TPb2p on posterior arm of Pb2 dorsally, continuous posteromedially with TEb2. TEb2 on dorsal surface of medialmost end of Eb2 near articulation with Pb3. TPb3, separated by large gap from TEb2, on Pb3 ventrolaterally, continuous posteromedially with TEb4. TEb4 on mid-posterior surface of Eb4 ventral to OD4 insertion and medial to OP, with which it joins a raphe laterally, and is continuous mid-posteriorly with SOD.

Remarks. A median longitudinal raphe extends from TPb2a to posterior margin of TEb2, and another extends from TPb3 to dorsoposterior margin of SOD. TPb2a is much narrower relatively than it is in *Lampanyctus*; it lacks the anterior portion without the median raphe.

OD3 lies dorsal to mid-section of OD4; origin on Pb3 dorsomedial edge dorsal to, and coincident with, origin of OD4 mid-section; insertion dorsoanteriorly on Eb3 uncinat process ventral to LE3 insertion.

OD4 origin extensive, beginning on Pb3 dorso-medial edge, passing dorsal to TPb3 and continuing

posteriorly ventral to OD3 origin, then dorsally to end of Pb3; insertion massive, on anterior surface of Eb4 levator process; posteroventrally joining raphe with OP.

OP a narrow strap; dorsally, narrowly on dorso-posterior Eb4 bony surface joining raphe laterally with OD4 insertion and medially with TEb4 attachment; ventrally on distalmost tip of Cb5, not interrupted by ER, which appears to be absent.

Ad1–3 absent.

Ad4 dorsally on posterolateral surface of Eb4, ventrally, narrowly on Cb4 just medial to inner angle formed by Eb4–Cb4 joint.

Ad5 narrowly on Eb4 posterodistally and Cb5 anterodistally.

RD comprising large RD ventrally and small RD' dorsally on each side. RD inserts completely separately from RD', attaching to posterior end of Pb4 and UP4; RD' joins longitudinal SO muscle layer at dorsoposterior end of Pb3 as layer divides bilaterally.

SOD present.

SO longitudinal muscle fibers appear to be restricted dorsally and ventrally in SO and originate at about horizontal between distal ends of Eb4s and extend anteriorly about to horizontal between distal ends of Eb3s.

Additional remarks. SCL absent. TV4 free from Cb5s. See also additional remarks under *Lampanyctus macdonaldi*. UP5 and Eb5 absent. Eb4 uncinat process absent.

Results—Pre-Acanthomorpha

Much of the raw data on the muscles is presented in Tables 1–6. The following discussion summarizes information for most of the muscles and assesses how the information bears on the pre-acanthomorph cladogram (Fig. 4). Muscle synapomorphies are italicized and numbered in parentheses, and summarized in Table 7. They are interpreted as such by parsimony based on how the character states are distributed among the taxa on the cladogram (for an example, see synapomorphy 9 below). We noted many cypriniform synapomorphies, but we include only those that occur homoplastically in other taxa (the two cyprinid genera we examined are closely related). We usually ignore autapomorphies of terminal taxa, but autapomorphies that might be interpreted as synapomorphies based on results of a total evidence analysis (not performed by us) are discussed. In some cases we have noted skeletal synapomorphies; these are not numbered nor indicated by italics.

(1) *Presence of Ads is a synapomorphy of Actinopterygii.*

(2) *Attachment of part of SO to a dorsal gill-arch skeletal element is a synapomorphy of Actinopteri.*

Polypterus is the only taxon in which SO does not attach to a dorsal gill-arch element.

(3) *Insertion of LE1 at dorsomedialmost end of Eb1 is synapomorphic for Osteoglossomorpha* (necessarily ignoring the two osteoglossomorph taxa that lack LE1 or in which it is unrecognizable, i.e., fused indistinguishably with another muscle). Among other pre-acanthomorphs, the insertion point of LE1 is quite variable, but with the exception of *Elops*, is always lateral to the medialmost end of Eb1. LE1 is rarely absent, and only autapomorphically.

(4) *Insertion of LE2 at dorsomedialmost end of Eb2 is synapomorphic for Osteoglossomorpha*. *Pantodon*, which is well nested among the osteoglossomorph clades on the basis of other evidence, is exceptional. Among the other pre-acanthomorphs, the insertion point of LE2 is quite variable, but with the exception of *Elops*, is always lateral to the medialmost end of Eb2. LE2 is rarely absent, and only autapomorphically, and the state is ignored in those taxa that lack it or in which it is unrecognizable, i.e., fused indistinguishably with another muscle.

(5) *Doubling of LE3 is a synapomorphy of Osmeroidea*. A doubling of LE3 (LE3, LE3') also occurs in some Clupeomorpha. LE3 is rarely absent, and only autapomorphically, except among Osteoglossomorpha, in which three of the ten genera examined lack the muscle or it is unrecognizable, i.e., indistinguishably fused with another muscle. See also (6) for Salangidae.

(6) *Doubling of LE4 (LE4, LE4') is a synapomorphy of Osmeroidea*. Too late for detailed inclusion, we examined the salangid *Protosalangichthys chinensis* (Osbeck), USNM 85840, and note that it also has LE3 and LE4 doubled. This corroborates Johnson and Patterson's (1996:307) inclusion of "salangids" with Osmeridae.

(7) *LP present is a synapomorphy of Clupeoidei*; see remarks following (8).

(8) *LP present is a synapomorphy of Characiformes*. LP has been reported for several diverse groups of pre-acanthomorph fishes, but we reserve the name for a muscle that inserts on Eb4, with or slightly separate from LE4, and originates "closely apposed to the surface of the epaxial body muscles [of clupeoids]" (Greenwood and Lauder, 1981:215), or on various cranial bones in all other groups that have it. Among pre-acanthomorphs, LP is restricted otherwise to *Chanos*, also a member of Otocephala. Although absent in *Denticeps*, currently recognized as the sister group of all other clupeomorphs, the presence of LP will probably be found to be synapomorphic for Otocephala. LP next appears in Lampriidiformes, first clade of Acanthomorpha. Levator posterior has been applied to a variety of morphologically similar but non-homologous muscles as the following discussion amply demonstrates.

Greenwood and Lauder (1981:228) stated that all of the otophysan taxa they examined, which included representatives of all four major groups (Fig. 4), have LP. We question the presence of LP in otophysans other than characiforms. The muscle Greenwood and Lauder identify as LP in cypriniforms is based on Winterbottom's interpretation (1974:254–256), and corresponds to our LCb5 (see Winterbottom's fig. 22a), which inserts on Cb5; that of siluriforms corresponds to our LI4 (see Winterbottom's fig. 21), which inserts on UP4. We are uncertain which gymnotiform muscle Greenwood and Lauder considered to be LP unless it is the muscle we identify as LE4 (inserts on Eb4), in which case they would consider LE4 as missing (see also Remarks following LI4 in description of *Diplomystes*). If future study should indicate that LE4 is absent in gymnotiforms, then absence of LE4 would appear to be a synapomorphy of siluriforms + gymnotiforms.

(9) *LII appears first in Ginglymodi and is a synapomorphy of Neopterygii*. From its first appearance, LII is the only levator that is present in all actinopterygian taxa we examined.

Lauder and Wainwright (1992:457) indicate that LIs are plesiomorphic for Chondrichthyes + Actinopterygii. We are unable to find the source on which they based their indication. LIs in Actinopterygii first appear in Neopterygii, are synapomorphic for that group, and cannot be plesiomorphic for Chondrichthyes + Actinopterygii: chondrichthyans have no levators originating on the cranium.

SPb1 first appears in Chondrostei and is a synapomorphy of Actinopteri. LII is attached to SPb1 when LII first appears in Ginglymodi. Halecomorpha and Osteoglossomorpha lack SPb1, so loss of SPb1 (and hence attachment of LII to it) is a synapomorphy of Halecostomi. SPb1 reappears in Elopomorpha and again LII is attached to it (condition present in both elopiform families and both albuliform families, but absent in all Anguillomorpha). Reappearance of SPb1 is a synapomorphy of Elopomorpha, but whether attachment of LII to SPb1 is also a synapomorphy is equivocal, because we do not know whether LII was attached to SPb1 in the ancestor of those forms that lack SPb1. The situation repeats. Loss of SPb1 (and attachment of LII to it) is a synapomorphy of Clupeocephala, but SPb1, with LI attaching to it, reappears in, and is a synapomorphy of, the clade Platytrichtidae + Alepocephalidae. The apparent conclusion to be drawn is that when both SPb1 and LII are present, LII attaches to SPb1.

(10) *Division of LII (our LIIa, LIIb) is a synapomorphy of Myctophidae*. First reported by Stiassny (1996:407), our data corroborate her findings. Presence of only LIIa in the myctophid *D. mollis* appears to be autapomorphic (see also remarks under LII in account of *D. mollis*).

(11) *LI2 appears first in Neopterygii and is a synapomorphy of that clade.* Aside from some specialized osteoglossiforms, LI2 is present in all but three, distantly related, pre-acanthomorph taxa that we examined.

(12) *Insertion of LI2 to include UP4 is a synapomorphy of Anguilliformes.* LI2 inserts primitively on Pb3, and as a specialization may insert on other skeletal elements.

(13) *LI3 is probably a synapomorphy of Teleostei.* LI3 appears first in Teleostei together with the first appearance of Pb4, on which it inserts primitively, and is probably a synapomorphy of that clade (but if not that clade, then of Osteoglossiformes and, independently, Elopoccephala). The problem in recognizing LI3 unequivocally as a synapomorphy of Teleostei is caused by the state of the LIs in *Hiodon*, which is the sister group of all other Osteoglossomorpha (= Osteoglossiformes), which, in turn, is the sister group of Elopoccephala (= all other Teleostei). *Hiodon* has only two LIs, LI1 and a second, relatively large LI, which may simply be LI2 or, conceivably, a fused LI2 and LI3. There are two possible scenarios: 1) the second LI represents only LI2, and LI3 has evolved independently in Osteoglossiformes and Elopoccephala; 2) the second LI represents fused LI2 and LI3 or only LI2, LI3 having been lost; the presence of LI3 would, thus, represent a teleostean synapomorphy. We prefer the second scenario for reasons that follow.

Osteoglossiformes, sister group of *Hiodon*, comprises two clades: Notopteroidei and Osteoglossoidi. Three of the four genera of notopteroids are highly specialized with many muscle fusions or losses, and LI2 and LI3 (if the latter was present) are either lost or indistinguishably fused with other muscles. The fourth genus, *Notopterus* and sister-group of the other three genera, has both LI2 and LI3. The character state for LI3 at the base of Notopteroidei is "LI3 present or?". Four of the five genera of Osteoglossoidi (including all three genera in the two basal-most clades) have LI2 and LI3 (the exception has only LI2). The character state for LI3 at the base of Osteoglossoidi is "LI3 present." Combining these two states, one concludes parsimoniously that the character state of LI3 for Osteoglossiformes is "LI3 present." The state for Hiodontiformes is, at its most conservative, "LI3 absent"; therefore, the character state for Osteoglossomorpha would be "LI3 present or absent." Given that "LI3 present" is the plesiomorphic state for Elopoccephala, combining the states for the two teleostean clades results parsimoniously in "LI3 present" as the (synapomorphic) character state for Teleostei.

(13a) *Insertion of LI3 to include Pb3 is a synapomorphy of Osteoglossoidi.* Among osteoglossomorphs, LI3, when present, inserts variously on Pb3 and Pb4, Pb4, or Pb3 and UP5. Pb4 is plesiomorphic,

therefore the insertion to include Pb3 is specialized. Insertion on UP5 is autapomorphic for *Pantodon*.

(14) *Absence of LI3 is a synapomorphy of Anguilliformes.*

(15) *Shift of the insertion of LI3 from Pb4 to UP5 is a synapomorphy of Neoteleostei.* See remarks following (16).

(16) *Loss of LI3 and UP5 is a synapomorphy of Ctenosquamata.* Johnson (1992) first hypothesized these two synapomorphies (15 and 16) and our findings corroborate his hypotheses.

TD is absent in *Polypterus*, possibly a result of loss or great reduction of Eb4. As such, it is not possible to decide if presence of TEb4 is a synapomorphy of Chondrostei or Actinopterygii; we assume the former (see 18).

(17) *Absence of attachment of TD to Eb4 is a synapomorphy of Albuliformes.*

(18) *Presence of TEb4 is a synapomorphy of Chondrostei.*

(19) *Presence of TEb4 is a synapomorphy of Clupeomorpha.*

(20) *Presence of TEb4 is a synapomorphy of Eurypterygii.*

(21) *Attachment of TD to include Pb2 is a synapomorphy of Gymnotiformes + Siluriformes.*

(22) *Attachment of TD to include Pb2 is a synapomorphy of Eurypterygii.*

(23) *Presence of TPb2a and TPb2b is a synapomorphy of Myctophiformes.*

(24) *Attachment of TD to Pb3 first occurs in Neopterygii, and is a synapomorphy of Neopterygii.*

(25) *Attachment of TD to Pb4 first occurs in Teleostei (where Pb4 first appears) and is a synapomorphy of Teleostei.*

(26) *Attachment of TD to Eb2 is a synapomorphy of Osteoglossoidi (Table 4).*

(27) *Attachment of TD to Eb2 is a synapomorphy of the unnamed clade: (Characiformes (Siluriformes, Gymnotiformes)).* Attachment of TD to Eb2 is plesiomorphic for Characiformes and present or absent in its sister group, Siluriformes (present) + Gymnotiformes (absent).

(28) *Attachment of TD to Eb2 is a synapomorphy of Neoteleostei.*

(29) *Presence of TEb2 is a synapomorphy of Neoteleostei.*

(30) *Presence of TEb2 is a synapomorphy of Osteoglossidae.*

(31) *OD4 first appears in Neopterygii, in which it attaches to Pb3, and is a synapomorphy of that clade.* After its first appearance, some component of OD4 (OD4' or OD4 as represented in the fused OD3–4) is rarely absent. See also (32–35).

(32) *OD3 first appears in Teleostei and is a synapomorphy of that clade.* An OD3 component (OD3 or OD3–4) is rarely absent.

(33) Except for the osteoglossomorph *Notopterus*, where it occurs homoplasiously, *some component of OD4 (OD4, OD4', OD3-4) first attaches to Pb4 in Elopocephala and is a synapomorphy of that clade* (Table 4).

(34) *Loss of attachment of an OD4 component (OD4, OD4', or OD3-4) to Pb4 is a synapomorphy of Neognathi* (Table 4). Absence of Pb4 in ateleopodids makes it impossible to polarize the group with regard to the origin of OD4. However, the origin of OD4 in ateleopodids is well anterior on Pb3 and would appear to indicate that it is highly unlikely that Pb4 would have participated in the origin; we assume this in our analysis of the synapomorphic states for (34) and (35).

(35) *Attachment of an OD4 component (OD4, OD4', or OD3-4) to Pb4 re-occurs in Stomiiformes and is a synapomorphy of that clade* (Table 4). See comments in (34).

(36) *A vertically oriented OD4 is a synapomorphy of Albuliformes.*

(37) *OP first appears in Halecomorpha and is probably a synapomorphy of Halecostomi.*

(38) *Absence of OP is a synapomorphy of Gonorynchiformes.* See comments in (40).

(39) *Absence of OP is a synapomorphy of Cypriniformes.* See comments in (34).

(40) *Absence of OP is a synapomorphy of Platytrichtidae + Alepocephalidae (two representatives of Alepocephaloidea).* OP frequently appears to be fused to SO and/or Ad5 and its presence is often questionable.

(41) *ER first appears in Teleostei and is a synapomorphy of that clade.* ER is often absent, and is never present when OP is unquestionably absent.

(42a) *Presence of RecD4 is probably a synapomorphy of Chondrostei.* RecDs are relatively uncommon among pre-acanthomorphs. RecD4 is absent in *Polypterus*, conceivably as a result of the loss or great reduction of Eb4. As such, it is not possible to decide with certainty if presence of RecD4 beginning with Chondrostei is a synapomorphy of Chondrostei.

(42) *Presence of RecD4 is a synapomorphy of Osteoglossomorpha.*

(43) *Presence of RecD4 is a synapomorphy of Cypriniformes.*

(44) *RecD2 first appears in Osteoglossiformes and is a synapomorphy of that clade.*

(45) *Presence of RecD2 is a synapomorphy of Cypriniformes.*

(46) *Presence of RecD2 is a synapomorphy of Anguilliformes.*

Bilaterally paired Pb muscles. The muscles of this group (Table 5) have their origins on Pbs and/or UPs and their insertions on Ebs and/or Cbs. These paired Pb muscles are not homologous with TD component muscles, which, in pre-acanthomorphs, do not be-

come divided bilaterally by losing their median portions, as they may in acanthomorphs. Furthermore, the paired Pb muscles are usually aligned longitudinally and, within a species, often have origins on the same Pbs and UPs as the TD muscles. Paired Pb muscles, which first appear in the Osteoglossomorpha, tend to be common only in Osteoglossomorpha and Anguillomorpha.

Concerning specific bilaterally paired Pb muscles:

(47) *Presence of M. Pb4-Eb2 is a synapomorphy of Osteoglossoidei.*

(48) *Presence of M. UP5-Cb4 is a synapomorphy of Albuliformes.*

(49) *Presence M. UP5-Cb4-Eb5 is a synapomorphy of Characiformes.*

(49a?) Ad1-3 are present in only three unrelated groups of pre-acanthomorphs: Polyodontidae, Notacanthidae, Cyprinidae. However, Edgeworth (1935: 131) reported that Ad1-4 are present in *Acipenser sturio* (not examined by us), but not *A. ruthenus*, *A. fulvescens*, and *Scaphirhynchus*. It is possible, therefore, that Ad1-3 are synapomorphic for Chondrostei.

(50) *Attachment of Ad5 to Eb5 (when Eb5 is present either as an autogenous element or when putatively fused with Eb4 or Cb4) is a synapomorphy of Teleostei.* This state is by far the most common among pre-acanthomorphs up to Neoteleostei. Ad5 is one of the most consistently present muscles and is always attached at its ventralmost or posteriormost end to Cb5. Among the taxa we examined it is unequivocally absent only in *Polypterus* and the eel, *Synphobranchus*, both of which lack Cb5. Only the attachments to other skeletal elements will be discussed further.

The primitive state for Ad5 in Actinopterygii is confused by the absence of the fifth arch in *Polypterus*, but it appears that the state is probably that of Ad5 attaching Cb5 to Cb4 (Table 6; *Acipenser*, *Atractosteus*, *Amia*). The primitive state appears autapomorphically above Halecomorpha in: Elopiformes, Anguilloidea, *Diplomystes*, *Lepidogalaxias*, Esocidae, *Ateleopus*, Aulopiformes, and *Neoscolepus*.

If attachment of Ad5 to Eb5 or to Eb4* (fused Eb5-Eb4) represents the same state (attachment to Eb5), then:

(51) *Attachment of Ad5 to Eb4 (in the absence of Eb5 or Eb4*) is a synapomorphy of Stomiiformes.* The state occurs otherwise, independently, only in Myctophidae, *Lepidogalaxias*, and in *Polyodon*.

(52) *Attachment of Ad5 to Eb4, when Eb5 is autogenous, is a synapomorphy of Cypriniformes;* it occurs otherwise, independently, only in *Searsia*.

(53) *Presence of RD is a synapomorphy of Neoteleostei.*

Wiley (1976:31) observed that RDs in amiids and lepisosteids are derived from the outer circular muscle layer of SO, in contrast to their derivation from

the inner longitudinal layer of SO in other fishes. Thus, he inferred that the RDs of amiids and lepisosteids are not homologous with RDs in other fishes, but can be interpreted as homologous in lepisosteids and amiids in having similar derivations. In opposition to that inference, Wiley (p. 32) also described several differences between the attachments of RDs in lepisosteids and amiids, and inferred that the state of the RDs in each of these two groups is autapomorphic, and thus their RDs are not homologous.

Plotting the distribution of RD on the cladogram (Fig. 4), disregarding the differing character states of RD in lepisosteids and amiids, indicates that some kind of RD is a synapomorphy of Neopterygii (but RDs lost is a synapomorphy in the next branch, Teleostei); thus, Wiley was justified in his first inference. Lacking knowledge of the particular characteristics of RD in the hypothetical neopterygian ancestor, there are three possibilities: RD resembled that of either extant lepisosteids or that of extant amiids or differed from both. His second inference, therefore, may be correct, but is unwarranted. The lack of homology at a higher phylogenetic level does not necessarily preclude homology at a lower level.

Another possibility is that the presence of RD may be a synapomorphy of Ginglymodi + Halecomorpha, which if corroborated by overall parsimony, will require rearrangement of these two clades in relation to Teleostei. (See also summary following this section.)

RD exhibits three states in pre-acanthomorphs we examined: RD completely dorsal to SO (SOD absent): *Amia*, *Atractosteus*, and *Lepidogalaxias* (all pre-Neoteleostei); RD completely ventral to SO (SOD absent): Ateleopodiformes and Aulopiformes (both Neoteleostei); RD and SOD present: *Pantodon* (pre-Neoteleostei) and Stomiiformes and Myctophiformes (Neoteleostei).

Three aulopiform taxa (*Gigantura chuni* Brauer, USNM 221034; *Omosudis lowei* Günther, USNM 206792; *Parasudis truculentus* (Goode and Bean), USNM 159095), in addition to those listed in Fig. 4, were examined. All agree with those listed in Fig. 4 in having RD completely ventral to SO. Although a very elongate RD was used to relate *Gigantura* to aulopiforms (i.e., synodontids, Rosen, 1983:440–441), the importance of RD being ventral to SO in pre-acanthomorphs has gone unnoticed, and offers additional support for a relationship of *Gigantura* to aulopiforms, but not specifically to synodontids. Based on the intermusculars, Johnson and Patterson (1995:31) placed *Gigantura* with alepisauroids within aulopiforms, and Baldwin and Johnson (1996) presented evidence that *Gigantura* and *Bathysaurus* form a sister group, which is the sister group of alepisauroids.

Presence of a ventral RD in Ateleopodiformes,

which forms a polytomy with Stomiiformes and Eurypterygii might be evidence to relate Ateleopodiformes with eurypterygian Aulopiformes. It is not possible, however, to polarize the ventral and dorsal states of RD. One character of RD, however, a single broad band of muscle that only divides at its attachment to the dorsal gill-arch skeleton, is unique to ateleopodids and some aulopiforms. At least *Aulopus*, which Baldwin and Johnson (1996:359) included in the basalmost aulopiform clade, and *Chlorophthalmus*, which they included in one of the next two aulopiform clades, share this state of RD with *Ateleopus*. Based on this evidence it is possible that Ateleopodiformes and Aulopiformes form a sister group, possibly resolving the Neoteleostean trichotomy. Such an arrangement would require addressing conflicts provided by synapomorphies (20 and 22), which support an aulopiform and ctenosquamate clade.

The presence of SOD basally in Acanthomorpha indicates that this state is plesiomorphic for Ctenosquamata. An aulopiform-ateleopodiform resolution of the neoteleostean trichotomy (Fig. 4), in which the new clade is the sister group of Ctenosquamata, would indicate that presence of SOD is a synapomorphy of Neoteleostei and its absence a synapomorphy of Aulopiformes + Ateleopodiformes.

(54) *Longitudinal SO muscle layer first appears in Halecostomi and is a synapomorphy of that clade.* We were unable to find a study on the composition of the SO muscle fibers in fishes and doubt that one exists. Indeed, the subject is rarely mentioned. Nevertheless, after discussion with several colleagues, we became aware that there is a generally erroneous concept that SO in fishes comprises an outer transverse muscle layer and an inner longitudinal muscle layer (e.g., Wiley, 1976:30–32). We find, however, that although an outer transverse layer is always present, a longitudinal layer is not. In some taxa, we were unable to determine on gross examination if a longitudinal muscle layer was present. Although we usually do not describe them, there are different distribution patterns of the longitudinal muscle fibers around the esophagus (e.g., the fibers may be concentrated dorsally and ventrally and absent laterally or they may be distributed more-or-less evenly around the esophagus). We suggest that a detailed histological study of the SO muscle layers is in order and would probably reveal important phylogenetic information.

(55) *Presence of TV4 is a synapomorphy of Halecostomi*, and, within the pre-acanthomorph portion of that clade, TV4 is absent only in the galaxioid *Retropinna*. Note: attachment of TV4 to Hb4 is an autapomorphy of Halecomorpha.

(55a) *Attachment of TV4 to Cb4 is a synapomorphy of Teleostei.* Note: Absence of Hb4 is also a synapomorphy of Teleostei.

(56) *Attachment of TV4 to Cb5 is a synapomorphy*

of *Cypriniformes*. Among pre-acanthomorphs, TV4 is primitively unattached to Cb5s. TV4 is attached to Cb5s in only three other pre-acanthomorph taxa, in each of which it is autapomorphic.

(57) *SCL first appears unquestionably in Albuliformes (= Albulidae) and is a synapomorphy of that clade.* Stiassny (1992:269) reported that the “semi-circular ligament system . . . is an innovation of the acanthomorph fishes,” by which she implied the first appearance of SCL (and the way in which RecV4 and ObV3 attach to it). She further stated (p. 270) that SCL is absent in pre-acanthomorphs. Stiassny is correct in indicating that SCL is primitively absent in pre-acanthomorphs, but it occurs in various pre-acanthomorph taxa. SCL is lacking in the most advanced pre-acanthomorphs, myctophiforms and most aulopiforms, but is present in the basalmost group of acanthomorphs, Lampridiformes. Only in the sense that its presence is homoplastic can it be considered to be an acanthomorph innovation.

(58?) *Presence of SCL is a synapomorphy of Elopomorpha*, if the condition of SCL in Elopiformes (see description in additional remarks in Elopidae) can be considered to indicate its presence. The differences in character states between Elopiformes and Albuliformes leaves unresolved which state is plesiomorphic.

(59?) *If SCL is considered to be absent in Elopiformes, the condition described in additional remarks in Elopidae is a synapomorphy of Elopiformes.*

(60) *SCL is a synapomorphy of the Esociformes.*

Summary (Table 7). The dorsal gill-arch musculature (and TV4 and SCL) provides support for monophyly of Actinopterygii and several of its currently recognized pre-acanthomorph clades. In general, support exists mainly for clades that are already well supported in the literature.

The dorsal gill-arch muscles provide conflicting evidence regarding the interrelationships of the Ginglymodi, Halecomorpha, and Teleostei. The monophyly of the Halecostomi (Halecomorpha + Teleostei) is supported by three synapomorphies: (37), presence of OP; (54), presence of SO longitudinal muscle layer; (55), presence of TV4. Alternatively, three synapomorphies conflict with halecostome monophyly and, instead, support the monophyly of the Halecomorpha + Ginglymodi: presence of RD, absence of attachment of TD to Eb4, and absence of RecD4. Thus, based on our muscle evidence, each hypothesis is equally parsimonious. The first is congruent with the generally accepted hypothesis expressed in our cladogram (Fig. 4). The second is congruent with the molecular evidence presented in Gardiner et al. (1996). We suggest that the interrelationships of Ginglymodi and Halecomorpha are worthy of additional study.

Hilton (2003) hypothesized a different set of interrelationships for Osteoglossoidei than the one in our Fig. 4. His classification exchanges the position

of Osteoglossidae (his Osteoglossinae) with that of Arapaimidae (his Heterotinae). His classification differs from ours only in aligning *Pantodon* as sister group of Osteoglossidae (his Osteoglossinae) instead of Arapaimidae (his Heterotinae). Given Hilton's arrangement, the major change would be that synapomorphy 13a would no longer be a synapomorphy of Osteoglossoidei, but would, instead, become a synapomorphy of Osteoglossidae. The other osteoglossomorph synapomorphies would remain the same.

Although not supporting monophyly of the two otocephalan clades, Ostariophysi and Clupeomorpha, two characters, the gongyloid cartilage (Di Dario, 2002) and LP are suggestive of close relationship of the clades, i.e., supportive of Otocephala. Among pre-acanthomorphs, the gongyloid cartilage is present only in *Chanos* (Ostariophysi) and most of the genera of Pristigasteroidea and Engrauloidea, (Clupeomorpha; see Additional remarks under *Chanos* and *Cetengraulis*). Similarly, among pre-acanthomorphs, LP is present only in characiform genera (Ostariophysi), *Chanos* (and possibly *Gonorynchus*, in which it was reported present by Greenwood and Lauder, 1981:228, although we did not find it), and all Clupeomorpha, except *Coilia* and *Denticeps*. It is also possible that LCB5A in cyprinids represents a modified LP.

There is evidence (not listed in Table 7) based on the state of RD and SO that Aulopiformes and Atelepodiformes form a clade, but other evidence may conflict.

Acanthomorpha

Additional material of acanthomorph taxa not mentioned in descriptive accounts (used for supplementary data, e.g., Table 8).

Cleared and stained. ACROPOMATIDAE: *Acropoma* sp., USNM 287444 (2); *Apogonops anomalus*, USNM 287447; *Doederleinia berycoides* (Hilgendorf), USNM 290474. AMBASSIDAE: *Ambassis* sp., USNM 218805 (4 specimens); *A. macleayi*, USNM 173817 (1). ARRIPIDAE: *Arripis georgianus* (Valenciennes), USNM 267149, 287442. CARANGIDAE: *Carangoides crysos* (Mitchill), USNM 167629; *Seriola* sp., USNM 306575; *Trachinotus falcatus* (Linnaeus), USNM 280104. CHAETODONTIDAE: *Chaetodon trifasciatus* Park, USNM 278739; *C. melannotus* Bloch and Schneider, USNM 266894; *Forcipiger flavissimus* Jordan and McGregor, USNM 340962; *Heniochus acuminatus* (Linnaeus), USNM 147893. COIIDAE: *Coilus* sp., USNM 269799. DINOLESTIDAE: *Dinolestes lewini* (Griffith and Smith), USNM 59932. DINOPERCIDAE: *Dinoperca petersi* (Day), USNM 269543. DREPANIDAE: *Drepane africana* Osorio, USNM 306264; *D. longimanus* (Bloch and Schneider), USNM 284472. EPHIPPIDAE: *Chaetodipterus zonatus* (Girard), USNM 220719, 220721; *Ephippus orbis*

Table 1.—Distribution of certain gill-arch muscles and SCL in genera of preacanthomorph fishes; homologies not implied. X = present; Y = present or absent; A = attached to Cb5; E = either OD3 or OD4 present, or only OD3–4 present; F = free from Cb5; L = longitudinal and transverse muscle layers present; T = only transverse muscle layer present; ? = presence or state questionable; * = state of L11.

Genera	LE1	LE2	LE2'	LE3	LE3'	LE4	LE4'	LP	L11	L11a*	L11p*	L12	L13	L13'	L14	OD2	OD3	OD3'	OD3-4	OD4	OD4'	OD4-4'	OP	OP'	ER	RecD2	RecD3	RecD4	RD	SO	SOD	TV4	SCL
<i>Diaphus</i>	X	X	X	X		X			X	X		X					X			X			X					X	L	X	F		
<i>Lampanyctus</i>		X		X		X			X	X	X	X					X			X			X		X			X	L	X	F		
<i>Neoscopelus</i>	X	X		X		X			X			X					X			X			X					X	L	X	F		
<i>Chlorophthalmus</i>	X	X		X		X			X			X	X				X			X			X					X	?		F		
<i>Saurida</i>	X	X		X		X			X			X	X				X			X			X		X			X	L		F		
<i>Aulopus</i>	X	X		X		X			X			X	X				X			X			X		X			X	?		F	X	
<i>Ateleopus</i>	X	X		X		X			X			X	X						X			X		X			X	L		F			
<i>Gonostoma</i>	X			X		X			X			X	X							X	X		X		X			X	L	X	F		
<i>Maurolicus</i>	X	X		X		X	?		X			X	X									X						X	?	X	F		
<i>Diplophos</i>	X	X		X		X			X			X	X				X			X	X		X					X	?	X	F		
<i>Umbra</i>	X	X		X		X			X			X	X				X			X			X		X				L		F	X	
<i>Dallia</i>	X	X		X		X			X			X	X				X			X			X						L		A	X	
<i>Novumbra</i>	X	X		X		X			X			X	X				E		E	E	X		X		X				L		F	X	
<i>Esox</i>	X	X		X					X			X	X				X				X		?		X				L		F	X	
<i>Searsia</i>	X			X		X			X			X	X	X			X			X	X								L		F	X	
<i>Alepocephalus</i>	X	X		X		X			X			X	X				X			X	X								L		F		
<i>Argentina</i>	X	X		X		X			X			X	X				X			X			X		X				L		F		
<i>Mallotus</i>	X	X		X	X	X	X		X			X	X				X			X			X		X				L		F		
<i>Hypomesus</i>	X	X		X	X	X	X		X			X	X				X			X			X		X				L		F	X	
<i>Lovettia</i>	X	X		X		X			X			X	X				X			X			X		X				?		F		
<i>Lepidogalaxias</i>	X	X		X		X			X			X		X			X			X	X		X		X			X	?		F		
<i>Galaxias</i>	X	X		X		X			X			X	X				X			X			X		X				L		F	A	
<i>Retropinna</i>	X	X		X		X			X			X	X				X		X	X	?		X		X				L		F		
<i>Coregonus</i>	X	X		X		X			X			X	X				X			X			X		X				L		A	X	
<i>Thymallus</i>	X	X		X		X			X			X	X				X			X			X		X				L		F	X	
<i>Oncorhynchus</i>	X	X		X		X			X			X	X				X	X		X			X		X				L		F	X	
<i>Gymnotus</i>	X	X		X		X			X			X	X				X			X					?				L		F		
<i>Diplomystes</i>	X	X		X		X			X			X	X		X		X			X			X		?				L		F		
<i>Xenocharax</i>	X	X		X		X		X	X			X	X		X		X		X	X			X		X				L		F		
<i>Brycon</i>	X	X		X		X		X	X			X	X				X			X	Y		X		X				L		F		
<i>Zacco</i>	X	X		X		X			X			X					X			X						X	X	X	L		A		
<i>Opsariichthys</i>	X	X		X		X			X			X					X			X						X	X	X	L		A		
<i>Gonorynchus</i>	X	X		X		X			X			X	X				X			X						X	X	X	L		A		
<i>Chanos</i>	X	X		X		X		X	X			X	X							X									L		F		
<i>Clupea</i>	X	X		X	X	X		X	X			X	X				X			X	X		?		Y				L		F		
<i>Dussumieria</i>	X	X		X	X	X			X	X		X	X				X			X	X		?		X				L		F		
<i>Chirocentrus</i>	X	X		X		X		X	X			X					X			X			X						L		F		
<i>Coilia</i>		X		X		X			X			X	X				X			X			X		X				L		F		
<i>Cetengraulis</i>	X	X		X		X		X	X			X	X				X			X			?						L		F		
<i>Ilisha</i>	X	X		X	X	X		X	X			X	X				X			X			X		X				L		F		
<i>Denticeps</i>	X	X		X		X			X			X	X				X			X			X		X				L		F		
<i>Synphobranchus</i>	X	X		X		X			X			X							X				?		X	X			L		F		
<i>Anguilla</i>	X	X		X		X			X			X					X			X			X		X	X	X		L		F		
<i>Conger</i>	X	X		X		X			X			X							X				X		X	X	X		L		F		
<i>Aldrovandia</i>	X	X		X		X			X			X	X						X				X						L		F		
<i>Notacanthus</i>	X	X		X		X			X			X							X				X						L		F		
<i>Pterothrissus</i>	X	X		X		X			X			X	X				X			X			X		X				L		F	X	
<i>Albula</i>	X	X		X		X			X			X	X				X			X			X	X	X				L		F	X	
<i>Elops</i>	X	X		X		X			X			X	X				X			X			X		X				L		F	?	
<i>Megalops</i>	X	X		X		X			X			X					X			X	X		X		X				L		F	?	
<i>Scleropages</i>	X	X		X		X			X			X	X				X			X			X		X	X			L		F		
<i>Osteoglossum</i>	X	X		X		X			X			X	X				X			X			X		X	X		X	L		F		
<i>Pantodon</i>		X		X		X			X			X	X						X				?				X	X	?	X	F		
<i>Arapaima</i>	X			X		X			X			X					X			X						X	X		?		F		
<i>Heterotis</i>	X	X		X		X			X			X	X		X		X			?					X				?		F		
<i>Mormyrus</i>	X	?		X					X			?	?				X						?		?	?	?		L		F		
<i>Petrocephalus</i>	X	X		X					X			?	?										?		?	X	X		L		F		
<i>Gymnarchus</i>	?	?							X																?	?	?		L		F		
<i>Notopterus</i>	X	X		X	X	X			X			X	X						X	X			?		X			X	L		F		
<i>Hiodon</i>	X	X		X		X			X			X	?			Y	X			X			X		X			X	L		F		
<i>Amia</i>	X	X		X		X			X			X								X			X		X				X	L		F	
<i>Atractosteus</i>	X	X		X		X			X			X								X								X	T				
<i>Polyodon</i>	X	X		X		X																					X	T					
<i>Acipenser</i>	X	X		X		X																					X	T					
<i>Polypterus</i>	X	X		X		X																							T				

Table 2.—Insertion sites or states of LI2 and LI3 and state of RD, if present, in genera of preacanthomorph fishes. X indicates insertion site or absence; ? = presence or absence questionable. Data for LI2 and LI2' combined for *Zacco*. 0 = RD dorsal to SO (SOD absent); 1 = RD ventral to SO (SOD absent); 2 = RD and SOD present. * = probably anomalous.

Genera	LI2								LI3						RD		
	Absent	Pb3	Pb4	UP3	UP4	UP5	Eb2	Eb3	Eb4	Absent	Pb3	Pb4	UP4	UP5		Eb3	Eb4
<i>Diaphus</i>		X									X						2
<i>Lampanyctus</i>		X									X						2
<i>Neoscopelus</i>		X									X						2
<i>Chlorophthalmus</i>		X										X		X			1
<i>Saurida</i>		X												X			1
<i>Aulopus</i>		X	X											X			1
<i>Ateleopus</i>		X									X			X			1
<i>Gonostoma</i>		X												X			2
<i>Maurolicus</i>		X												X			2
<i>Diplophos</i>		X												X			2
<i>Umbra</i>		X										X					
<i>Dallia</i>		X										X					
<i>Novumbra</i>		X										X					
<i>Esox</i>		X										X					
<i>Searsia</i>		X	X									X					
<i>Alepocephalus</i>		X										X			X*		
<i>Argentina</i>		X										X					
<i>Mallotus</i>		X										X					
<i>Hypomesus</i>		X										X					
<i>Lovettia</i>		X										X					
<i>Lepidogalaxias</i>	X											X					0
<i>Galaxias</i>		X										X					
<i>Retropinna</i>		X										X					
<i>Coregonus</i>		X										X					
<i>Thymallus</i>		X										X		X			
<i>Oncorhynchus</i>		X										X		X			
<i>Gymnotus</i>		X					X	X				X	X				
<i>Diplomystes</i>			X		X							X	X			X	
<i>Xenocharax</i>		X										X					
<i>Brycon</i>		X										X					
<i>Zacco</i>		X					X	X		X							
<i>Opsariichthys</i>		X					X	X		X							
<i>Gonorynchus</i>		X										X					
<i>Chanos</i>		X										X					
<i>Clupea</i>		X										X					
<i>Dussumieria</i>		X					X					X	X				
<i>Chirocentrus</i>	X											X					
<i>Coilia</i>		X										X					
<i>Cetengraulis</i>		X										X					
<i>Ilisha</i>		X										X					
<i>Denticeps</i>		X										X					
<i>Synaphobranchus</i>		X			X	X				X							
<i>Anguilla</i>					X					X							
<i>Conger</i>		X		X	X					X							
<i>Aldrovandia</i>		X										X		X			
<i>Notacanthus</i>		X								X							
<i>Pterothrissus</i>		X											X	X			
<i>Albula</i>		X											X	X			
<i>Elops</i>		X										X					
<i>Megalops</i>	X											X					
<i>Scleropages</i>		X									X	X					
<i>Osteoglossum</i>		X									X	X					
<i>Pantodon</i>		X									X			X			2
<i>Arapaima</i>		X								X							
<i>Heterotis</i>		X	X									X					
<i>Mormyrus</i>	?									?							
<i>Petrocephalus</i>	?									?							
<i>Gymnarchus</i>	X									X							
<i>Notopterus</i>		X	X									X					
<i>Hiodon</i>		X	X														
<i>Amia</i>		X								X							0
<i>Atractosteus</i>		X								X							0
<i>Polyodon</i>	X									X							
<i>Acipenser</i>	X									X							
<i>Polypterus</i>	X									X							

Genera	TPb1-Eb2																TPb2-Pb3-Eb1-Eb2								TPb2-Pb3-Eb4							TPb2-Pb3-Pb4							TPb2-Pb3-Pb4-Eb4							TPb2-Pb3a							TPb3							TPb3-Eb4							TPb3-Eb4-UP3-UP4							TPb3-Pb4							TPb3-UP3-UP4							TPb3a							TPb3-Eb2							TPb3a-Eb2							TPb3p							TPb3p-Pb4							TPb3p-Pb4-Eb4							TPb3p-UP4							TPb3'							TPb4							TPb4-Eb3							TPb4-Eb4							TUP4a							TUP4p							TUP5						
	TEb1-Eb2	TEb2	TEb2a	TEb2p	TEb2v	TEb3	TEb4	TPb1-Pb2-Pb3-Eb1-Eb2	TPb2	TPb2a	TPb2p	TPb2-Pb3-Eb4	TPb2-Pb3-Pb4	TPb2-Pb3-Pb4-Eb4	TPb2-Pb3a	TPb3	TPb3-Eb4	TPb3-Eb4-UP3-UP4	TPb3-Pb4	TPb3-Pb4-Eb4	TPb3-UP3-UP4	TPb3a	TPb3-Eb2	TPb3a-Eb2	TPb3p	TPb3p-Pb4	TPb3p-Pb4-Eb4	TPb3p-UP4	TPb3'	TPb4	TPb4-Eb3	TPb4-Eb4	TUP4a	TUP4p	TUP5																																																																																																																																																						
<i>Diaphus</i>	X					X			X	X					X																																																																																																																																																																										
<i>Lampanyctus</i>	X					X			X	X					X																																																																																																																																																																										
<i>Neoscopelus</i>	X					X			X	X					X																																																																																																																																																																										
<i>Chlorophthalmus</i>	X					X								X											X																																																																																																																																																																
<i>Saurida</i>	X				U	X		U																																																																																																																																																																																	
<i>Aulopus</i>	X					X								X											X				U	X																																																																																																																																																											
<i>Ateleopus</i>	X														X																																																																																																																																																																										
<i>Gonostoma</i>	X														X																					X																																																																																																																																																					
<i>Maurollicus</i>		U	U															X																		X																																																																																																																																																					
<i>Diplophos</i>	X			U											X																					X																																																																																																																																																					
<i>Umbra</i>															X				X																																																																																																																																																																						
<i>Dallia</i>															X																																																																																																																																																																										
<i>Novumbra</i>																								X																																																																																																																																																																	
<i>Esox</i>																							X																																																																																																																																																																		
<i>Searsia</i>																							X																																																																																																																																																																		
<i>Alepocephalus</i>																							X																																																																																																																																																																		
<i>Argentina</i>																			X																																																																																																																																																																						
<i>Mallotus</i>																				X																																																																																																																																																																					
<i>Hypomesus</i>																																																																																																																																																																																									
<i>Lovettia</i>													U																																																																																																																																																																												
<i>Lepidogalaxias</i>																																																																																																																																																																																									

*Polypterus***

Table 4.—Skeletal elements to which TD attaches (Eb4 undifferentiated from Eb4*; see also Table 3) and relation of OD4 (and/or OD4' or OD3-4; see also synapomorphies (30-40) in Results section) to Pb4 in genera of preacanthomorph fishes. A = Pb4 absent; P = Pb4 present, but TD not attached to it; X = attached to; ** = TD absent; 1 = origin at least partly on Pb43; 2 = Pb4 present, but origin not on it.

Genera	Skeletal elements											OD4
	Eb1	Eb2	Eb3	Eb4	Pb1	Pb2	Pb3	Pb4	UP3	UP4	UP5	
<i>Diaphus</i>		X		X		X	X	P				2
<i>Lampanyctus</i>		X		X		X	X	P				2
<i>Neoscopelus</i>		X		X		X	X	P				2
<i>Chlorophthalmus</i>		X		X		X	X	X				1
<i>Saurida</i>		X	X	X		X		P				2
<i>Aulopus</i>		X		X		X	X	P				2
<i>Ateleopus</i>		X					X	A				A
<i>Gonostoma</i>		X						P		X		1
<i>Maurolicus</i>		X					X	X				1
<i>Diplophos</i>		X					X	P		X		1
<i>Umbra</i>				X			X	X				2
<i>Dallia</i>							X	X				2
<i>Novumbra</i>							X	X				1
<i>Esox</i>							X	X				1
<i>Searsia</i>				X			X	X				1
<i>Alepocephalus</i>				X			X	X				1
<i>Argentina</i>							X	X				2
<i>Mallotus</i>				X			X	X				1
<i>Hypomesus</i>		X		X			X	X				1
<i>Lovettia</i>				X		X	X	X				1
<i>Lepidogalaxias</i>							X	P				2
<i>Galaxias</i>				X			X	X				2
<i>Retropinna</i>				X			X	X				1
<i>Coregonus</i>				X			X	X				1
<i>Thymallus</i>				X			X	X				1
<i>Oncorhynchus</i>				X			X	X				1
<i>Gymnotus</i>				X		X	X	X				1
<i>Diplomystes</i>	X	X			X	X	X	X				1
<i>Xenocharax</i>		X		X			X	X				2
<i>Brycon</i>		X		X			X	X				1
<i>Zacco**</i>								A				A
<i>Opsariichthys**</i>								A				A
<i>Gonorynchus</i>				X			X	X				1
<i>Chanos</i>				X			X	P				2
<i>Clupea</i>				X			X	X				1
<i>Dussumieria</i>				X			X	X				1
<i>Chirocentrus</i>				X			X	X				1
<i>Coilia</i>			X	X			X	X				1
<i>Cetengraulis</i>				X			X	X				1
<i>Ilisha</i>				X			X	X				2
<i>Denticeps</i>		X		X			X	X				1
<i>Synaphobranchus</i>							X	A	X	X		A
<i>Anguilla</i>				X			X	A	X	X		A
<i>Conger</i>				X			X	A				A
<i>Aldrovandia</i>							X	X				1
<i>Notacanthus</i>		X		X			X	A				2
<i>Pterothrissus</i>							X	X				1
<i>Albula</i>							X	P		X		1
<i>Elops</i>				X			X	X				1
<i>Megalops</i>				X			X	X				1
<i>Scleropages</i>		X		X			X	X				2
<i>Osteoglossum</i>		X		X			X	X				2
<i>Pantodon</i>	X	X		X			X	A				A
<i>Arapaima</i>		X		X			X	X				2
<i>Heterotis</i>							X	X				2
<i>Mormyrus</i>				X			X	X				2
<i>Petrocephalus</i>				X			X	X				2
<i>Gymnarchus</i>				X		X	X	A				A
<i>Notopterus</i>				X			X	X				1
<i>Hiodon</i>				X			X	X				2
<i>Amia</i>							X	A				A
<i>Atractosteus</i>							X	A				A
<i>Polyodon</i>				X				A				A
<i>Acipenser</i>				X				A				A
<i>Polypterus**</i>								A				A

Table 5.—Distribution of bilaterally paired pharyngobranchial muscles in suprageneric groups of preacanthomorph fishes (all genera within each group are included). X = present; * = not illustrated.

Suprageneric Groups	M. Pb2-Eb1	M. Pb2-Eb2	M. Pb3-Eb3	M. Pb3-Eb3-Eb2	M. Pb3-Pb4-Eb2	M. Pb4-Eb2	M. Pb4-UP5-Eb2	M. UP4-Eb2	M. UP4-Eb4	M. UP4-Eb5-Cb4	M. UP5-Cb4	M. UP5-Cb4-Eb5
Aulopiformes												
<i>Chlorophthalmus</i>												
<i>Saurida</i>		X										
<i>Aulopus</i>												
Stomiiformes												
<i>Gonostoma</i>											X	
<i>Maurollicus</i>												
<i>Diplophos</i>												
Esociformes												
<i>Umbra</i>												
<i>Dallia</i>												
<i>Novumbra</i>			X									
<i>Esox</i>												
Characiformes												
<i>Xenocharax</i>												X*
<i>Brycon</i>												X*
Elopomorpha												
<i>Synphobranchus</i>		X										
<i>Anguilla</i>	X											
<i>Conger</i>	X								X			
<i>Aldrovandia</i>							X					
<i>Notacanthus</i>												
<i>Pterothrissus</i>											X	
<i>Albula</i>								X			X	
<i>Elops</i>												
<i>Megalops</i>												
Osteoglossomorpha												
<i>Scleropages</i>							X					
<i>Osteoglossum</i>		X				X						
<i>Pantodon</i>		X										
<i>Arapaima</i>						X						
<i>Heterotis</i>						X						
<i>Mormyrus</i>	X				X							
<i>Petrocephalus</i>	X				X							
<i>Gymnarchus</i>				X								
<i>Notopterus</i>												
<i>Hiodon</i>												

(Bloch), USNM 257868; *Platax orbicularis* (Forsskal), USNM 268668. EPIGONIDAE: *Sphyrænops bairdianus* Poey, USNM 270279. HAEMULIDAE: *Haemulon sexfasciatus* Gill, USNM 292785. LOBOTIDAE: *Lobotes pacificus* Gilbert, USNM 82008. MONODACTYLIDAE: *Monodactylus argenteus* (Linnaeus), USNM 266897. PEMPHERIDAE: *Parapriacanthus ransonneti* Steindachner, USNM 218867; *Pempheris schwenkii* Bleeker, USNM 269801. PERCICHTHYIDAE: *Bostockia porosa* Castelnau, USNM 218841; *Gadopsis marmoratus* Richardson, USNM 214836, 308109 (2). POMACANTHIDAE: *Centropyge bicolor* (Bloch), USNM 56995; *Pomacanthodes semicirculatus* (Cuvier), USNM 273043. SCATOPHAGIDAE: *Scatophagus argus* (Linnaeus), USNM 224393 (3), 259383; *Selenetoca multifasciata* (Richardson), USNM 173514, 245702 (2). SCORPIDIDAE: *Microcanthus strigatus* (Cuvier), USNM 267047; SIGANIDAE: *Siganus vulpinus* (Schle-

gel and Müller), USNM 325277. TRICHIURIDAE: *Trichiurus lepturus* Linnaeus, USNM 272931.

Muscle preparations in alcohol. APLODACTYLIDAE: *Crinodus lophodon* (Günther), USNM 227300. CARANGIDAE: *Decapterus macrosoma* Bleeker, USNM 307977; *Decapterus punctatus* (Cuvier), USNM 199037; *Selene vomer* (Linnaeus), USNM 338012. CENTRARCHIDAE: *Acantharchus pomotis* (Baird), USNM 237611; *Ambloplites rupestris* (Rafinesque), USNM 333731; *Archoplites interruptus* (Girard), USNM 39563; *Centrarchus macropterus* (Lacepède), USNM 243775; *Lepomis auritus* (Linnaeus), USNM 243888; *Pomoxis annularis* Rafinesque, USNM 129524. CHAETODONTIDAE: *Chaetodon austriacus* Rüppell, USNM 267044. CHIASMODONTIDAE: *Chiasmodon* sp., USNM 1186139. GEMPYLIDAE: *Neopinnula americana* (Grey), USNM 366716; *Promethichthys prometheus* (Cuvier), USNM 289930.

Table 6.—Character states for Eb5 and skeletal elements (other than Cb5) to which Ad5 attaches in genera of preacanthomorph fishes. 0 = Eb5 absent; 1 = Eb5 autogenous; 2 = Eb5 putatively fused to Eb4 (based on configuration of distal end of Eb4); 3 = Eb5 putatively fused to Cb4; X = major attachment; x = minor attachment. Eb5 character state 2 for Osteoglossomorpha reassessed in "Epibranchials 5 and 4" under section "Muscles and Skeletal Elements."

Genera	Eb5	Skeletal elements					
		EB4	EB4*	EB5	Cb4	Cb4*	AC
<i>Diaphus</i>	0	X					
<i>Lampanyctus</i>	0	X					
<i>Neoscopeus</i>	0				X		
<i>Chlorophthalmus</i>	1			X	X		
<i>Saurida</i>	0				X		
<i>Aulopus</i>	1			X	x		
<i>Ateleopus</i>	0				X		
<i>Gonostoma</i>	0	X					
<i>Maurolicus</i>	0	X					
<i>Diplophos</i>	1	X		X			
<i>Umbra</i>	1			X			
<i>Dallia</i>	0				X		
<i>Novumbra</i>	0				X		
<i>Esox</i>	0				X		
<i>Searsia</i>	1	X					x
<i>Alepocephalus</i>	1			X			
<i>Argentina</i>	1			X			
<i>Mallotus</i>	2		X				
<i>Hypomesus</i>	2		X				
<i>Lovettia</i>	2		X				
<i>Lepidogalaxias</i>	0	x			x		
<i>Galaxias</i>	2		X				
<i>Retropinna</i>	2		X				
<i>Coregonus</i>	1			X			
<i>Thymallus</i>	1			X			
<i>Oncorhynchus</i>	1			X			
<i>Gymnotus</i>	1			X			
<i>Diplomystes</i>	1			X	X		
<i>Xenocharax</i>	1			X			
<i>Brycon</i>	1			X			
<i>Zacco</i>	1	X					
<i>Opsariichthys</i>	1	X					
<i>Gonorynchus</i>	2		x				X
<i>Chanos</i>	1			X			
<i>Clupea</i>	2		X				
<i>Dussumieria</i>	1			X			
<i>Chirocentrus</i>	2		X				
<i>Coilia</i>	2		X				
<i>Cetengraulis</i>	2		?				
<i>Ilisha</i>	2		X				
<i>Denticeps</i>	1			X			
<i>Synphobranchus</i>	0	Ad5 absent					
<i>Anguilla</i>	0				X		
<i>Conger</i>	0				X		
<i>Aldrovandia</i>	1			X	X		
<i>Notacanthus</i>	1 or 2			X	X		
<i>Pterothrissus</i>	1				X		
<i>Albula</i>	3						X
<i>Elops</i>	1			X	X		
<i>Megalops</i>	1			X	x		
<i>Scleropages</i>	2		X				
<i>Osteoglossum</i>	2		X				
<i>Pantodon</i>	1			X			
<i>Arapaima</i>	2		X				
<i>Heterotis</i>	2		X				
<i>Mormyrus</i>	2		X				
<i>Petrocephalus</i>	2		X				
<i>Gymnarchus</i>	2		X				
<i>Notopterus</i>	2		X				
<i>Hiodon</i>	2		X				
<i>Amia</i>	0					X	
<i>Atractosteus</i>	0					X	
<i>Polyodon</i>	0	X					
<i>Acipenser</i>	0					X	
<i>Polypterus</i>	0	Ad5 absent					

INERMIIIDAE: *Inermia vittata* Poey, USNM 318643. ISTIOPHORIDAE: *Istiophorus* sp., USNM 22999. KYPHOSIDAE: *Kyphosus sectatrix* (Linnaeus), USNM 116955. MONODACTYLIDAE: *Monodactylus argenteus* Linnaeus, USNM 258894 (3), 266897. NOTOGRAPTIDAE: *Notograptus guttatus* Günther, USNM 173798. POMACANTHIDAE: *Centropyge bispinosus* (Günther), USNM 336476; *C. vrolikii* (Bleeker), USNM 210295. SCATOPHAGIDAE: *Scatophagus argus* (Linnaeus), USNM 224393. SCOMBRIDAE: *Gasterochisma melampus* Richardson, TMH D.1982; *Euthynnus alletteratus* (Rafinesque), USNM 214658; *Scomberomorus cavalla* (Cuvier), USNM 289928; *S. commersoni* (Lacepède), USNM 297407. SCORPIDIDAE: *Scorpius* sp., USNM 339348. SIGANIDAE: *Siganus spinus* (Linnaeus), USNM 233575. TRACHTERIDAE: *Trachipterus* sp., USNM 346705.

Lampridiformes

VELIFERIDAE

Velifer hypselopterus Bleeker, NSMT-P-59516, 30°S, 168°E. 165 mm.

Plate 59

Additional material. ② = *Metavelifer multiradiatus* (Regan), AMS I.20605013, ca. 94 mm SL; USNM 23953, cleared and stained.

Remarks. AMS specimen dissection was faulty, but muscles, except for TEb2 and ODs, appear to be remarkably similar to *V. hypselopterus*.

Description.

LE1 on Eb1 mid-dorsoposteriorly beginning lateral to base of uncinat process.

LE2 on Eb2 mid-dorsoposteriorly.

LE3 on anterior margin of cartilaginous tip of Eb3 uncinat process, just dorsal to OD3.

LE4 slender tendinous insertion on tip of Eb4 levator process.

LP absent, possibly represented by discrete ligamentous attachments, two on Eb4 levator process, one on Eb3 uncinat process, that fuse into broad sheet of fascia dorsally, which is also continuous with sheet of fascia representing PP.

LI1 on Pb2 just ventroposterior to large dorsal, cartilage-tipped process.

LI2 on Pb3 dorsolaterally anterior to medial end of Eb3.

TD comprises completely separate TEb2 and broad, more-or-less continuous TPb3-Pb4-Eb3-Eb4 (attachments distinct laterally), which is posteriorly continuous with SOD. TEb2 consists of two, discontinuous parts. Left-side TEb2 originates as broad-dorsal and slender-ventral muscle straps (ventral strap not visible in Plate 59) attached to thick CT pad enveloping right-side Pb2 and Pb3 cartilaginous artic-

Table 7.—Synapomorphies (as numbers), based on dorsal gill-arch muscles, TV4, and SCL, supporting Actinopterygian preacanthomorph fish groups (see Results section for explanation).

Group	Synapomorphy number
Ctenosquamata	16
Myctophiformes	23
Myctophidae	10
Eurypterygii	20, 22
Neotelostei	15, 28, 29, 53
Stomiiformes	35, 51
Esociformes	60
Neognathi	34
Platytrichtidae +	
Alepocephalidae	40
Osmeroidea	5, 6
Characiformes +	
Siluriformes +	
Gymnotiformes	27
Gymnotiformes +	
Siluriformes	21
Characiformes	8, 49
Cypriniformes	39, 43, 45, 52, 56
Gonorynchiformes	38
Clupeomorpha	19
Clupeoidei	7
Elopomorpha	58?
Anguilliformes	12, 14, 46
Albuliformes	17, 36, 48, 57
Elopiiformes	59?
Elopocephala	33
Teleostei	13, 25, 32, 41, 50, 55a
Osteoglossomorpha	3, 4, 42
Osteoglossiformes	44
Osteoglossoidae	13a, 26, 47
Osteoglossidae	30
Halecostomi	37, 54, 55
Neopterygii	9, 11, 24, 31, 42a?, 49a?
Chondrostei	18
Actinopteri	2
Actinopterygii	1

ulating processes (pad mostly removed in Plate 59) and attaches to dorsomedial surface of left-side Eb2 anterior to LE2 insertion. Right-side TEb2 originates medially from CT on left side and passes laterally between dorsal and ventral straps of left-side TEb2 and inserts similarly on right-side Eb2. TPb3-Pb4-Eb3-Eb4 attaches to bony dorsoposterior surface of Pb3 and dorsomedial surfaces of Eb3 and Eb4 and dorsoanterior surface of Pb4. ② TEb2 damaged in dissection, but could have been continuous across gill arches, with anterior edge attaching to CT pad enveloping Pb2 and Pb3 processes.

Remarks. The specialized medial overlapping of TEb2 on each side was seen only in *Lampris* and *Velifer*, and supports close relationship of these two taxa. The condition in *Metavelifer* should be verified.

OD3 and OD4 originate together on dorsoanterior bony surface of Pb3 and separate at about their mid-length before inserting broadly on anterior surface of Eb3 uncinat process and dorsomedial edge of Eb4

uncinate process. ② Both muscles consist of loose strands, but appear to be separate distal to their origins.

OP dorsally on posterior surface of Eb4 medial to dorsal attachment of Ad4 and ventrally on dorsodistal surface of Cb5 just posterior to posterior attachment of Ad5.

Ad1–3 absent.

Ad4 attaches dorsally to posterolateral surface of Eb4 and ventrally to Cb4 dorsally just anterior to inner angle of Eb4-Cb4 joint.

Ad5 attaches anteriorly to Cb4 posterodistal end and AC4 posteriorly, and posteriorly to Cb5 distal end anterior to ventral attachment of OP.

SOD present.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to cartilaginous ventroposterior tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC absent. CT pad enveloping Pb2 and Pb3 processes gives rise to CT strap that attaches to cranium. AC4 and a much smaller AC3 present. Medial ends of Eb4 and Eb3 about equal in size. ② AC3 and AC4 absent; medial ends of Eb3 and Eb4 about equal in size.

Olney et al. (1993) hypothesized that the Veliferidae are the sister group of all other lampridiforms and that the Trachipteridae and Regalecidae are the most specialized. The Veliferidae lack ER as does the Trachipteridae (based on *Trachipterus* sp., USNM 346705).

LAMPRIDAE

Lampris guttatus (Brünnich), SIO82-70, not measured (estimate >300 mm).

Plate 60

Description.

LE1 on anterior surface of posterior bony flange of Eb1, cartilage-tipped uncinat process absent.

LE2 on anterior surface of posterior bony flange of Eb2 just anterolateral to LE2' insertion (see remarks following LE2').

LE2' on dorsal edge of posterior flange of Eb2, anterior surface appressed to posterior surface of LE2, muscle fibers of LE2 and LE2' extend dorsally at different angles.

Remarks. Right-side LE2' cleanly separable from LE2, but left-side pair did not separate cleanly. Verification of distinctness in other, smaller specimens needed.

LE3 sheet-like, on tip of Eb3 uncinat process anteriorly, muscle continuous dorsoposteriorly with presumed LE4-LP complex.

LE4 broad sheet, muscous distally, fascial proximally, inserting on Eb4 levator process, continuous ventrolaterally in fascia with presumed LP fibers; fas-

cia continues ventrodistally around fourth arch and attaches to Cb5 distally.

LP presumably represented by small strap of fibers arising from fascia at posterolateral edge of LE4 fibers (information from right side only; left side damaged); posterior fascia presumably continuous with PP.

LI1 on Pb2 dorsoanterolaterally.

LI2 on Pb3 dorsoanterolaterally.

TD comprises TEb2 and TEb3-Eb4. TEb2 with distinct right- and left-side muscle straps, each inserting on respective Eb2 mid-dorsoanteriorly, anterior to LE2 insertion; straps originate medially from ventral surface of thick CT pad enveloping anterior cartilaginous anterior ends of Pb2s and Pb3s and dorsally from CT attaching to Pb3; left-side strap passes through right-side strap before attaching to CT; muscle extends laterally and attaches on Eb2 dorsoanteriorly anterior to LE2 insertion. TEb3-Eb4 attaches to dorsomedialmost surface of Eb3, dipping to level below that of attachment to dorsomedialmost surface of Eb4.

Remarks. CT permeating TD obscures attachments; insertions should be verified on smaller specimen.

OD3 origin on Pb2 dorsoanteriorly, more-or-less continuous with OD4 origin, divides laterally with one branch, OD3, inserting on Eb3 uncinat process, and the other branch, OD3', inserting on Eb3 dorsoanterior surface.

OD4 origin on Pb3 dorsoanteriorly; left-side inserts on Eb4 levator process; right side inserts on both Eb3 uncinat and Eb4 levator processes.

OP dorsally broadly on Eb4 posteriorly ventral to tip of uncinat process and extending laterally; ventral extent unclear.

Ad1-3 absent.

Ad4 questionably absent (unusual if true), but if present, much reduced, possibly represented by muscle fibers obscured from view by OP.

Ad5 on Cb5 distally and Cb4 posterodistally at ventral attachment of Ad4.

SOD broad.

RDs adjacent.

Additional remarks. SCL present, attached mid-dorsally to posteroventral cartilaginous tip of Bb3. TV4 damaged, appears to have had a median septum, apparently free from Cb5s. IAC absent. Pb4 and UP4 present. Eb4 uncinat process absent. Pb2 toothed. Tiny AC2 present on left side, absent on right side. PCI insertion restricted well medial to distal end of Cb5; muscles unusual in that right and left sides join together anteromedially.

Polymixiiformes

POLYMIXIIDAE

Polymixia lowei Günther, USNM 159295, 89.3 mm,
USNM 202153, 124 mm.

Plate 61

Description.

LE1 broadly on anterior surface of Eb1 uncinat process just lateral to cartilage tip.

LE2 on dorsoposterior edge of Eb2 just posterolateral to lateral end of TEb2.

LE3 on tip of Eb3 uncinat process just dorsal to insertion of OD3-4 on Eb3.

LE4 on Eb4 surrounding small Eb4 levator process, ventrolaterally continuous with broad PP fascia.

LP slender, tendinously inserted among LE4 fibers basally.

LI1 broadly on Pb2 dorsal surface just anteromedial to base of Pb2 uncinat process.

LI2 on bony Pb3 dorsoposterolaterally meeting TPb3-Eb3 insertion anteriorly.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 with straps attaching to dorsal surface of cartilaginous and bony anterior end of Pb2 just anterior to LI1 insertion, lies dorsal to TEb2 anteriorly, and is complexly continuous ventrally with TEb2, and also posteriorly by diagonal muscle slip with TEb2. TEb2 broad, with crossing straps extending mid-anteriorly from attachments with TPb2 ventral surface and inserting on Pb2 anteriorly, but muscle mainly inserting on Eb2 dorsoanteromedialmost surface, at most reaching to opposite medial edge of LE2 insertion; muscle continuous posteriorly by crossing muscle slips with TPb3-Eb3. TPb3-Eb3 inserting on Pb3 dorsoposteriorly, meeting anteromedial edge of LI2 insertion, and on Eb3 dorsomedially.

OD3-4 originating broadly on Pb3 bony dorsal surface ventral to TEb2, inserting on Eb3 bony surface anteriorly beginning just ventral to tip of uncinat process and on posterior bony surface of Eb4 beginning just ventral to uncinat process.

OP strap of muscle on Eb4 dorsoposteriorly ventral to LE4 insertion and medial to Ad4 on Eb4, ventrally on Cb4 joining raphe (ER) with Ad5.

M. SO-Pb3 (indicated, but not labeled on Plate 61 as broad strap of longitudinal SO fibers lateral to each RD) extends anteriorly, passing ventral to TPb3-Eb3 and inserting on Pb3 dorsally anterior to RD insertion.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteriorly, ventrally on Cb4 medial to Eb4-Cb4 joint.

Ad5 ventrally broadly on Cb5 dorsally beginning at dorsodistal tip and extending medially; dorsally joining ER with OP ventrally at attachment of both on Cb4. Tendinous tissue extends laterally from ER and is continuous with PP fascia, which attaches around Eb4-Cb4 distally (incompletely indicated in Plate 61).

SOD slender, continuous anteriorly by fine, diagonal muscle slip with TPb3-Eb3 posteriorly.

RDs slender, juxtaposed.

Additional remarks. SCL attached mid-dorsally to ventroposterior cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC absent. Pb2 toothed.

Paracanthopterygii

Percopsiformes

Percopsiform monophyly and intrarelationships.—Rosen (1962) implied the monophyly of the Percopsidae + Amblyopsidae + Aphredoderidae, which subsequently became known as the Percopsiformes (Greenwood et al., 1966:396). Later, Rosen (1985: 42–45) was first to question the monophyly of the percopsiform fishes, removing the Percopsidae, but aligning aphredoderids with amblyopsids on the basis of their thoracic anus and segmented premaxilla. Patterson and Rosen (1989:19–20) reaffirmed Rosen's (1982) findings, stating that they could find no character synapomorphous for the Percopsiformes [of Rosen, 1962]. They failed to note, however, that among their many illustrations of paracanthopterygian dorsal gill-arch skeletons, the medial head of Eb4 of percopsiforms is much broader than the combined breadth of the medial heads of any two other epibranchials (first noted by Parenti (1993:181), who interpreted the character as a synapomorphy of atherinomorphs, percopsids, amblyopsids, and aphredoderids). Among the other paracanthops, the medial head of Eb4 is comparatively narrow, and in only a few macrourid gadiforms, which are well removed from the percopsiforms in Patterson and Rosen's cladogram (1989:fig. 16), is the percopsiform condition approximated.

An additional character, not noted previously, is the presence of a levator process on the percopsiform Eb4, which is present in some or all members of the three families (e.g., the process is absent in *Amblyopsis* (Patterson and Rosen, 1989:figure 13E), but present in *Chologaster*—both Amblyopsidae, thus, we consider the process primitively present in percopsiforms). The process is lacking in all other paracanthops and present elsewhere among non-percomorph acanthomorphs only in Lampridae, *Polymixia*, and the zeiform *Xenolepadichthys*.

Murray and Wilson (1999) hypothesized a Percopsiformes comprising only percopsids and aphredoderids. They placed the amblyopsids as a deeply embedded clade in the Anacanthini, which they placed as the sister group of Percopsiformes. They based their classification on 47 osteological characters and included fossil taxa. They also overlooked the enlarged medial head of epibranchial 4 as a possible character, and simply disposed of the position of the anus and segmented premaxilla, which Rosen (1985) had used to unite aphredoderids and amblyopsids, by

stating, “The new placement of the amblyopsids requires viewing these characters as homoplasies [!].”

Based on the three percopsiform taxa we examined (*Aphredoderus sayanus*, Aphredoderidae; *Percopsis omiscomaycus*, Percopsidae; *Chologaster agassizi*, Amblyopsidae) the group shares the following specializations:

1. OD4' (a branch of OD3–4) extending posteriorly, passing dorsal to jointly articulating Eb3 and Eb4 uncinat processes, and inserting on Eb4 levator process. We have not found this muscle in any other acanthomorph.

2. OD origin includes Pb3 (mainly) and Pb2. OD only originates on Pb3 in most other acanthomorphs; exceptions include: platycephalids, percids, caproids (*Capros*, but not *Antigonia*), elassomatids, gasterosteids (only *Apeltes*), and hypoptychids.

3. M. Pb2-Eb2 present. This is an uncommon muscle with a spotty occurrence otherwise among fishes (e.g., we found it in the distantly related paracanthop family Ophidiidae, and the percoids: *Morone*, Moronidae, and *Sillago*, Sillaginidae. Endo (2002:101, as OD2) reported that it is generally absent in gadiforms, but present in lotines, gaidropsarines, phycines, most gadines, and the morid *Lotella*. He (2001:fig. 34) illustrated the musculature of *Gaidropsarus* and and gadiform bregmaceratid, *Bregmacerops*).

4. TEb2 absent. TEb2 is usually present in acanthomorphs, but is notably absent in some other Paracanthopterygii and in all Atherinomorpha (but present in Mugilomorpha, i.e., *Agonostomus*, Mugilidae, hypothesized sister group of the atherinomorphs (Stiassny, 1993; Johnson and Patterson, 1993).

5. LE3 absent. Occurs variously among fishes, but is not common, except among Smegmamorpha and Polycentridae.

6. Medial end of Eb4 much enlarged relative to medial end of Eb3 (also common in many smegmamorphs, but not mugilomorph Mugilidae).

7. Levator process present on Eb4. This process otherwise occurs variously among acanthomorphs, but uncommonly among pre-Percomorpha.

8. An overall trapezoidal appearance, in dorsal view, of the combined transverses dorsales and obliqui dorsales. We have not seen such configuration in any other fishes.

The combination of these specializations almost certainly indicates the monophyly of the percopsiforms. The presence of characters 4–6 commonly among Smegmamorpha, suggests that the percopsiforms and smegmamorphs, may be more closely related than current classifications indicate, a relationship most recently suggested by Parenti (1993). The absence of all three of these characters in the Mugilidae, would seem to preclude such relationship.

Evidence from the gill-arch muscles is equivocal

for resolving percopsiform intra-relationships. Absence of an OD attachment to Eb3 is a specialization shared only by *Chologaster* and *Percopsis*. Conversely, absence of a TPb3 attachment is a specialization shared only by *Chologaster* and *Aphredoderus*. Non-musculature characters, however, such as the advanced anus and segmented premaxilla shared by *Aphredoderus* and *Chologaster*, strongly favor a hypothesis that they are the sister group of *Percopsis*.

APHREDODERIDAE

Aphredoderus sayanus (Gilliams), USNM 238477, 71.3 mm; USNM 238466, 69.0 mm.

Plate 62

Description.

LE1 on and medial to small, sharp prominence at base of Eb1 uncinat process.

LE2 on tip of expanded bony process on posterior edge of Eb2.

LE3 absent.

LE4 on Eb4 levator process dorsoanteriorly, joining raphe medially with OD4 insertion and another laterally with LP insertion.

LP insertion continuous with LE4 insertion ventrolaterally.

LI1 on Pb2 anteriorly, ventromedial surface joining raphe with TPb2 just dorsal to LI1 insertion.

LI2 broadly on Pb3 dorsolaterally, narrowly on Pb4 anterolaterally and adjacent dorsoanterior edge of UP4.

TD comprises TPb2 (TPb2d + TPb2v), and TEb4. TPb2d dorsal to TPb2v, each sheetlike, united anteriorly; muscles together are pad-like and notched mid-anteriorly, each with mid-longitudinal raphe, which join together mid-anteriorly. CT sheet overlies TPb2d raphe and is attached to it; TPb2d fibers form heart-shaped curve; TPb2d fibers curve broadly anteriorly; muscles attach together on anteromedialmost surface of Pb2 uncinat process, joining raphe there with LI2, but continuing ventromedially to insert on anterolateralmost surface of Pb2 (insertion visible only in ventral view after removal of underlying tissues). TEb4 triangular, apex anteriorly with fibers variously joining SO longitudinal fibers and CT in midline, posteriorly almost divisible transversely into two sections, anterior section maintains triangularity, posterior section more strap-like, two sections joining laterally and attaching along most of posterior margin of Eb4 levator process, there joining raphe with OP.

M. Pb2-Eb2 on Pb2 uncinat process and dorsal surface mostly ventral to OD3-4, extending laterally and inserting on most of dorsal surface of Eb2.

OD unusually broad dorsoanteriorly, comprises OD4' dorsally and OD3-4 ventrally; OD4' and OD3-4 originate inseparably, broadly on Pb3 and Pb2 ventral to TPb2; OD4' extends posterolaterally

over joined Eb3 and Eb4 uncinat processes (but is not attached to them) and inserts on anterior surface of Eb4 levator process, where it joins raphe with ventroanterior edge of LE4; OD3-4 splits off ventrally shortly posterior to joint origin with OD4' and inserts on Eb3 uncinat process, with remaining portion passing ventral to joined Eb3-Eb4 uncinat processes and inserting on Eb4 anterior surface medial to insertion of OD4'.

Remarks. It is unusual for OD to attach to Pb2.

OP dorsally on Eb4 posterior surface at and medial to levator process, joining raphe there with TEb4, ventrally on Cb5 dorsolaterally, ventrolaterally joining raphe with Ad5.

Ad1-3 absent.

Ad4 on most of Eb4 posterior surface (medial half of muscle anterior to OP) and distal half of Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally on posterolateralmost two-fifths of Cb4 and ventrally on anterodistalmost end of Cb5, joining raphe medially with OP.

SOD absent.

RDs separate, adjacent.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Pb3 toothed. IAC absent.

PERCOPSIDAE

Percopsis omiscomaycus (Walbaum), USNM 179711, 92.3 mm; USNM 334972, 72.1 mm.

Plate 63

Description (based on larger specimen with remarks on smaller specimen).

LE1 on small bony prominence near base of Eb1 uncinat process.

LE2 on expanded posterior edge of Eb2.

LE3 absent.

LE4 tendinously on dorsal tip of Eb4 levator process.

LP on lateral surface of tendinous insertion of LE4 and distalmost end of Eb4. Smaller specimen with LP inserting only on tendinous insertion of LE4.

LI1 on dorsoanteriormost surface of Pb2.

LI2 on Pb3 dorsolaterally.

TD comprises TPb2 and TPb3-Eb4. TPb2 roughly heart-shaped, notched anteriorly, with median raphe (from which CT sheet arises dorsally), lies dorsal to Pb3 portion of TPb3-Eb4, but not continuous with it, comprises two scarcely separable parts (more obvious in smaller, non-illustrated specimen) possibly equivalent to TPb2d and TPb2v of *Aphredoderus*; anterior part on dorsoanteriormost end of Pb2 and medial surface of uncinat process of Pb2; posterior part attaches to posterior surface of Pb2 uncinat process and forms raphe there with M. Pb2-Eb2. TPb3-Eb4 broadly triangular, blunted apex anterior, long side posterior, with irregular median raphe in anterior

three-fourths, attaching by few muscle straps to Pb3 posteromedially; long side slender laterally, attaching along most of Eb4 dorsal arm, forming raphe laterally with dorsal end of OP.

Remarks. Left-side OP of large specimen comprises two separate straps, lateral and medial. Right side has only lateral strap, with muscle area occupied by medial strap on left side forming part of SO. In smaller specimen, OP is broad, single, and occupies joint area of OP on left side of larger specimen.

M. Pb2-Eb2 originates on Pb2 uncinat process at raphe with TPb2 posterior part and attaches along most of bony dorsal surface of Eb2.

OD3 absent.

OD unusually broad dorsoanteriorly, comprises OD4' and OD4. OD4' originates broadly on Pb3 bony dorsal surface ventral to TPb2, passes dorsal to joined Eb3 and Eb4 uncinat processes, and inserts on Eb4 levator process just medial to LE4 insertion. OD4 originates on Pb2 dorsally ventrolateral to OD4', joins OD4' just distal to origins, passes ventromedial to joined Eb3-Eb4 uncinat processes, and inserts on anterior surface of distal end of Eb4 ventral to OD4' insertion. In smaller specimen OD4 and OD4' are mostly fused, separating only just anterior to their insertions on Eb4.

OP dorsally on posteromedial surface of Eb4, joining raphe there with Eb4 portion of TPb3-Eb4, ventrally forming raphe with Ad5 before both attach dorsodistally to Cb5. No raphe with Ad5 in smaller specimen. See also remarks following TD.

Ad1-3 absent.

Ad4 on distal half of ventral surface of Eb4, partially anterior to OP, and ventrally on Cb4 distal half medial to Eb4-Cb4 joint.

Ad5 on posterodistal end of Cb4 and dorsodistal end of Cb5 forming raphe ventromedially with OP just before attaching to Cb5. No raphe with OP in smaller specimen.

SOD broad.

RDs adjacent.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Tiny AC between right-side Pb2 and Eb1 uncinat processes of larger specimen, possibly represents vestigial IAC, but IAC coded as absent for this taxon.

AMBLIOPSIDAE

Chologaster agassizii Putnam, USNM 232514, 65.4 mm.

Plate 64

Description.

LE1 on Eb1 uncinat process about mid-dorsoposteriorly; medial process absent.

Remarks. Typically in acanthomorphs the medial

Eb1 process articulates with Pb1, and the uncinat process with Pb2 or IAC, which articulates with Pb2.

LE2 beginning on about mid-dorsoposterior bony edge of Eb2 and extending posteriorly onto CT between Eb1 and Eb2 (mostly on CT).

LE3 absent.

LE4 on Eb4 beginning at levator process anteriorly and extending laterally along dorsoposterior edge of OD4 insertion, and just medial to LP insertion.

LP on Eb4 distally, anterior and slightly lateral to lateral edge of LE4 insertion.

LI1 on Pb2 anterolaterally (at anteriormost junction of Pb2 and Pb3).

LI2 on Pb3 dorsolaterally.

TD comprising TPb2d, TPb2v, and TEb4. TPb2d a transverse strap, with median raphe ventrally attached to CT lining pharynx, laterally attached to Pb2 just dorsoposterior to LI1 insertion and continuous and just anterior to TPb2v attachment. TPb2v a diagonal strap on each side extending anterolaterally from raphe with posterior end of OD4' on Pb3 on one side and attaching to Pb2 just posterior to TPb2d on opposite side, some muscle strands passing through strands of contralateral TPb2v; asymmetrically continuous with TEb4. TEb4, roughly triangular in shape, apex anterior, commencing along common line with OD4' posteromedially, and extending posterolaterally; muscle strands, somewhat interlaced, becoming continuous with horizontal posterior portion of muscle, and inserting on Eb4 dorsoposteriorly; forming raphe with dorsal end of OP.

Remarks. We have arbitrarily equated the two Pb2 sections of *Chologaster* with TPb2d and TPb2v of *Aphredoderus* (see also *Percopsis*).

M. Pb2-Eb2 originating on dorsoanterior edge of Pb2 (where it articulates with Eb1 medial end) and inserting along most of bony dorsal surface of Eb2.

OD3 absent.

OD comprises OD4' and OD4, extremely broad dorsally and deep ventromedially, originating on Pb3 dorsomedially, continuing onto Pb2 dorsolaterally ventral to TPb2v. Muscle joins raphe posteromedially with posteromedial end of TPb2v of opposite side and divides posterolaterally into OD4' and OD4, with OD4' passing posteriorly dorsal to joined Eb3 and Eb4 uncinat processes and inserting on Eb4 levator process just ventral (anterior in view) to LE4 insertion and lateral to TEb4 attachment, and OD4 passing ventral to joined Eb3-Eb4 uncinat processes and inserting on Eb4 dorsally medial to levator process.

OP dorsally, broadly on posterior surface of Eb4, ventrally on dorsodistal end of Cb5 joining Ad5; medially continuous with SO.

Ad1-3 absent.

Ad4 on most of dorsal surface of Eb4 anterior to OP attachment, and on distal half of surface of Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally on posterodistal fourth of Cb4, with slight tendinous extension to posterodistal end of Eb4; ventrally on distal end of Cb5, ventromedially joining raphe with OP.

SOD present.

RDs slightly separated.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. IAC absent.

Ophidiiformes

OPHIDIIDAE

Dicrolene intronigra Goode and Bean, USNM
362587, 2 specimens, 226–240 mm TL.

Plate 65

Description.

Remarks. Only one of the two sets of gill arches was dissected to expose hidden muscle attachments, and the description of these is based mostly on that specimen. The remainder of the description is based on the undissected specimen.

LE1 on anterior surface of Eb1 uncinat process ventrolateral to tip.

LE2 on tip of prominent bony process on posterior margin of Eb2, insertion continuous posteriorly as ligament joining Eb2 with Eb3.

LE3 on Eb3 uncinat process just ventrolateral to tip, meeting insertion of OD3 portion of OD3–4.

LE4 tendinously on dorsal edge of Eb4 lateral to uncinat process and immediately dorsal to Ad4 attachment.

LP absent.

LI1 on dorsomedial edge of Pb2 joining raphe with TPb2p laterally and M. Pb2-Eb2 medially.

LI2 on Pb3 dorsoposteromedially lateral to M. SO-Pb3 and RD; passes medial to OD3–4.

TD complex, comprises TPb2, TPb2p, TPb3, TEb3, and, variably, TPb4 (absent in illustrated specimen). TPb2 very broad transversely, slender longitudinally, on bony edge lateral to cartilaginous edge of dorsal margin of broad Pb2 dorsal process (entire edge is cartilaginous in other specimen), continuous broadly posteriorly with TPb2p but overlapping TPb2p anterolaterally on right side (both sides non-illustrated specimen). TPb2p much shorter longitudinally than TPb2, passes dorsal to OD3–4 origin, touching LI1, then extends ventrally medial to LI1 and attaches on dorsomedial edge of Pb2; joins partial raphe with ventromedial surface of LI1; continuous by diagonal muscle strands with TPb3. TPb3 on dorsal surface Pb3 mid-laterally medial to lateral cartilaginous process articulating with small AC (not illustrated) between process and medial end of Eb2 (posteromedial cartilage-tipped process of Pb2 is ventral to ACs and attached to them ventrally); continuous posteriorly by diagonal muscle strands with

very broad TEb3. TEb3 dorsomedially on Eb3 bony surface beginning slightly lateral to medial cartilaginous end, continuous posteriorly by diagonal muscle strands with narrow TPb4 (TPb4 absent in illustrated specimen, in which case continuous with SOD). TPb4 extends deeply laterally and attaches finely to Pb4 dorsomedial surface; continuous posteriorly by diagonal strands of muscle with SOD.

M. Pb2-Eb2 on posterior edge of Pb2 dorsal process, just meeting lateral edge of TPb2 and the lateral edge of LI1 insertion, and on posterior surface of raised anterior edge of Eb2 just anteromedial to LE2.

OD3–4 origin on dorsoanterior surface of Pb3, divides posteriorly at mid-length or just before inserting narrowly on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process. On left side of illustrated specimen, an anomalous strap of OD3–4 attaches to Pb2 at the junction of LI1 and M. Pb2-Eb2.

OP dorsally on Eb4 posterior surface below and medial to uncinat process, ventrally joining raphe (ER) with Ad5 dorsolaterally where both attach to medial end of CT pad enveloping posterolateral end of Cb4 (medial end of pad well separated from distal end of Cb4).

M. SO-Pb3, longitudinal-fiber band originating from SO in region of Eb4 and extending anteriorly ventral to TD components and inserting on Pb3 just ventral to RD (q.v.).

Ad1–3 absent.

Ad4 dorsally on dorsoposteriormost edge of Eb4 beginning at and ventral to medial end of LE4 insertion and ending slightly medial to distal end of Eb4; ventrally on Cb4 dorsal surface medial to Eb4-Cb4 joint.

Ad5 dorsolaterally joining raphe (ER) with OP on fleshy CT pad enveloping distal end of Cb4, medially on posterior surface of lateral fourth of Cb5, joining raphe there with TV5

SOD present.

RDs well separated, extending far anteriorly ventral to TD components and inserting on Pb3 just posterior to OD3–4 origin.

Additional remarks. SCL absent. TV4 in two unconnected parts; anterior part with strong mid-longitudinal raphe, originating on Cb4s ventral to posterior part and attaching mid-dorsoanteriorly to ventral surface of cartilaginous Bb4; ventral part continuous, originating on Cb4s dorsoposterior to anterior part, free from Cb5s. We have seen this type of TV4 elsewhere only in the lophiiform *Chaunax* (Chaunacidae), which differs in that a fine muscle strand joins the two portions and the two halves of the anterior portion are separate at their attachment to the large cartilaginous Bb, which may be Bb4 or a complex.

The dorsal tips of both Pb1s are cartilaginous in one specimen and bony in the other. Pb4 and UP4

present. IAC present. Eb4 levator process absent. Pb2 toothed. Medial end of Eb3 and Eb4 about same size.

There is a separate ball of cartilage between the medial end of Eb2 and the cartilage-tipped process mid-laterally on Pb3. Markle (1989:fig. 1A) illustrated the dorsal gill-arch skeleton of a specimen he identified as the neobythitine *Dicrolene intronigra*. The illustration does not accord with the skeleton of our two specimens. For instance, he shows Eb2 articulating with Pb2 and does not indicate the presence of an accessory cartilage either between this articulation or one attached to Pb3. Nor does he show a cartilage-tipped process mid-laterally on Pb3. Patterson and Rosen (1989:fig. 13g) illustrated the dorsal gill-arch skeleton of *Monomitopus torvus* Garman (another neobythitine), which is very similar to that of our specimens of *D. nigra*. Consequently, one of the characters (contact between Eb2 and Pb2) Markle used to define a gadiform-batrachoidiform relationship apparently is invalid or needs modification.

Brotula multibarbata Temminck and Schlegel,
USNM 340397, 166 mm, 214124, 133 mm.

Not illustrated

Description.

LE1 on highest point of raised dorsoposterior bony edge of Eb1, uncinat process lacks cartilaginous tip.

LE2 on apex of prominent raised dorsoposterior bony edge of Eb2.

LE3 on dorsoanterior surface of Eb3 uncinat process lateral to cartilaginous tip.

LE4 on bony dorsoposterior edge of Eb4 well lateral to uncinat process, fibers of posterior surface attaching on dorsal edge of CT covering Eb4 posterior surface.

Remarks. Dorsolateral fibers of OP and dorsomedial fibers of Ad4 attach to same CT ventrally. Releasing CT from Eb4 results in strip of muscle (= LE4-OP sling of Stiassny and Jensen, 1987) interrupted by band of CT.

LP absent.

LI1 on Pb2 dorsolaterally ventromedial to TPb2 attachment to Pb2; larger than LI2.

LI2 on dorsoposterolateral surface of Pb3 just medial to medial head of Eb3; muscle passes amidst OD3-4 dividing it into OD3-4 and OD4 (see OD3-4).

TD comprises TPb2, TPb2p, TEb2, and TEb3. TPb2 a bean-shaped pad, covered with thin CT, attachment beginning anteriorly with CT of roof of pharynx, continuing laterally and ending on anteriormost cartilaginous tip of Pb2, free edge continuing posterolaterally from this point and overlying all OD components anteriorly; muscle attached ventrally to dorsoanterior surface of Pb3 together with OD inser-

tions; broadly continuous posteriorly with TPb2p. TPb2p on Pb2 dorsolaterally at and medial to M. Pb2-Eb2 origin, posteriorly broadly continuous with TEb2. TEb2 on Eb2 dorsoanteriorly well medial to LE2 insertion, forming short raphe with ventral edge of M. Pb2-Eb2 insertion and posterolateralmost edge of OD2 insertion, broadly continuous posteriorly with TEb3. TEb3 on dorsal surface of Eb3 medial to base of uncinat process; broadly continuous posteriorly with SOD.

OD comprises OD2, OD3-4, and OD3'. All OD components originate together on Pb3 dorsoanteriorly; components separate shortly distal to origin, with OD3-4 being variously split by penetration of LI2 on its way to its insertion and recombining as they insert on Eb3 and Eb4; on anterior and posterior surfaces, and medial edge of Eb3 just ventral to tip of uncinat process, fusing ventrally with dorsal origin of RecD3; on anterior surface and medial edge of Eb4 just ventral to tip of uncinat process, meeting OP dorsally. OD3' inserts on Eb3 dorsally ventral to OD3-4 insertion on Eb3, continuous there with ventral origin of RecD3.

OD2 inserts on raised dorsoanterior edge of Eb2 immediately ventral to M. Pb2-Eb2, there joining raphe with RecD3 insertion; posterolateralmost edge of OD2 forming short raphe with TEb2.

OP with two slightly separated attachments on Eb4 posterior surface; dorsomedial attachment on uncinat process, posteriorly overlapping ventrolateral attachment on Eb4 lateral to uncinat process, fusing together before ventrally joining raphe with dorsolateral end of Ad5 (CT extension from raphe continues onto Cb4 posterior surface and posteroventral fibers of Ad4 join raphe). Also see remarks under LE4.

M. Pb2-Eb2 tendinously on anteriormost cartilaginous tip of Pb2, to which TPb2 and Eb1 uncinat process attach; broadly, muscoulously on Eb2 dorsoanterior edge.

RecD3 with two separate origins, dorsal origin on Eb3 uncinat process ventral to and fusing with OD3-4, ventral origin on dorsoanterior edge of Eb3, both parts fusing and inserting on Eb3 along insertion line of OD2.

Ad1-3 absent.

Ad4 on Eb4 posterior surface lateral to OP, ventrally on Cb4 dorsoposteriorly, attaching to CT extending from ER. Also see remarks under LE4.

Ad5 broadly on dorsodistal edge of Cb5, narrowing dorsally and joining raphe, which continues as CT on Cb4, with OP; attachment to Cb4 is well medial to distal end.

SOD present.

RDs present, separated.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Pb1 with cartilaginous

ends. Pb2 toothed. Medial end of Eb3 larger than that of Eb4. IAC absent.

BYTHITIDAE

Calompteryx jeb Cohen, USNM 208341, 57.6 mm.
Not illustrated

Description.

LE1 on Eb1 mid-dorsoposteriorly, anterior (pharyngobranchial supporting) process absent.

Remarks. Anterior process considered absent (uncinate present) because medial end of Eb1 articulates with Pb2.

LE2 on Pb2 posteriorly a little lateral to mid-length, just lateral to lateral end of M.Pb2-Eb2.

LE3 on Eb3 just lateral to cartilage tip of uncinate process.

LE4 on Eb4 dorsoposteriorly between uncinate process and distal tip of Eb4.

LP absent.

LI1 broadly on Pb2 dorsoanterolaterally, ventromedially joining raphe with TPb2 laterally, larger than LI2.

LI2 penetrating OD3–4, dividing it into almost two equal portions, and separating TPb3 posteriorly from TEb3, while passing ventral to TEb3 on way posteriorly to insertion on Pb3 dorsoposteriorly near medial end of Eb4.

Remarks. Penetration of OD3–4 by LI2 is uncommon. Occurs also in related Ophidiidae and Carapidae, and unrelated Champodontidae and Odontobutidae (synapomorphic for all genera of latter).

TD comprising TPb2, TPb3, and TEb3. TPb2 broad, flat, thin, attaching to Pb2 beginning at anterior end and extending posteriorly to medial edge of LI2, attached anteroventrally to CT of pharyngeal roof, dorsally infiltrated with filmy CT, which covers TD, continuous posteriorly by diagonal muscle strands with TPb3. TPb3 slender, extends ventrolaterally and slightly anteriorly anterior to LI2 (as latter extends ventroanteriorly from origin) and attaches to Pb3 dorsally anterior to medial end of Eb3, continuous mid-dorsoposteriorly with TEb3. TEb3 broad mid-dorsally, extending narrowly laterally, passing dorsal to LI2 (as latter extends ventroanteriorly from origin) and attaches moderately broadly on Eb3 dorsomedially, broadly continuous mid-dorsoposteriorly with SOD.

M. Pb2-Eb2 medially broadly on Pb2 laterally beginning at anterior end and extending posteriorly to LI1 insertion, laterally on Eb2 dorsally, reaching medial edge of LE2 insertion.

OD3–4 anteriorly, broadly on Pb3 dorsoanteromedially, almost completely divided longitudinally by passage of LI2, posteriorly on Eb3 dorsoanteriorly beginning immediately ventral to fine cartilage tip of uncinate process, there meeting LE3 insertion ante-

roventrally, and on medial edge and posterior surface of Eb4 uncinate process.

OP dorsally, broadly on Eb4 posteriorly beginning ventral to uncinate process and extending medially, ventrally joining ER on Cb4 with Ad5 dorsally, dorsolaterally slightly overlapping Ad4 medially, which is also on Eb4 a little ventral to level of OP attachment.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly, beginning medially just anteroventral to lateral edge of OP and extending laterally to end of Eb4, ventrally on Cb4 dorsally, beginning near lateral end and extending medially anterior to OP.

Ad5 ventrally on Cb5 distally, joining ER dorsally with OP ventrally on Cb4, beginning well medial to distal end of Cb4 and continuing medially.

SOD present.

RDs separated by distance less than one RD diameter, extending far anteriorly and inserting on Pb3s dorsally.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 absent, UP4 present. Pb2 toothed. Pb1 absent. IAC absent. Medial end of Eb3 larger than that of Eb4. PCI begins attachment to Cb5 well medial to distal end of Cb5, attaches by moderately long tendon to cleithrum.

CARAPIDAE

Not examined.

Remarks. Vandewalle et al. (1998) briefly described and illustrated the gill-arch skeleton and musculature of the Carapidae. The publication was available to us only as a poor quality photocopy. Nevertheless, several important features were apparent. Some of the specializations they report (LP absent, LI2 penetrates OD, etc.), are shared with bythitids and some ophidiids.

All levators originate on inner surface of the hyomandibula (we did not take note of the origins in our dissections of other ophidioids, which Vandewalle et al. noted would be of interest).

LE1–LE4 present.

LP absent.

LI1 present (their LINT 2/3 or LINT3) inserting on Pb2 and Pb3 or Pb3, depending on genus.

LI2 (their LINT4) inserting on “Pb4” (probably UP4, presence of cartilaginous Pb4 not mentioned), penetrates OD3, which they recognize as OD3s and OD3p.

IAC absent, but IAB (with cartilaginous ends) present, which Vandewalle et al. term an “interarcual element.” Eb1 uncinate process apparently absent.

TPb2, TEb2, and TEb3 present.

OD1,2,3s,3p,4. Originating variously on Pb2, Pb2,

Pb2 and 3, Pb4 [= UP4?], respectively, and inserting on Eb1, Eb2, Eb3, Eb3, Eb4 respectively.

OP originating on Pb4 [= UP4?] or Eb4 depending on genus, and inserting on Cb5.

RecDs [their REDOs]. RecD1 origin on Pb2, insertion on IAB; RecD2, origin on IAB, insertion on Eb2; RecD3 origin on Eb2, insertion on Eb3; RecD4, origin on Eb3, insertion on Eb4.

Ad1–3 apparently absent.

Ad4 apparently absent, but should be verified.

Ad5 on distal end of Cb5 and on Eb4 (and in one genus, also on Eb3).

SOD apparently absent.

RDs originate on second and third vertebrae, insert at front of Pb3s.

TV4 present, not attached to Cb5s.

Gadiformes

Endo (2002) published a phylogenetic study of the of the Gadiformes. He discussed very little about the dorsal gill-arch musculature, but mentions (2000:82), following other authors, that TDA comprises only TEb2 in the gadiforms he examined. He (2002:fig. 34) only illustrates (partially) the dorsal gill arch musculature of *Gaidropsarus* (Gadropsaridae) and *Bregmaceros* (Bregmacerotidae). The musculature of *Gaidropsarus* is similar to that of *Raniceps* and *Opsanus* (a batrachoidiform) in lacking LE3, but includes M. Pb2-Eb2 (labelled as OD2), which neither of the other two genera have. Endo (2002:101) noted that M. Pb2-Eb2 “is generally absent in most gadiforms, but present in lotines, gaidropsarines, phycines, gadines (except *Gadiculus*, *Brosme*) and the morid *Lotella*.” His illustration of *Bregmaceros* also shows that it lacks LE3, as well as M. Pb2-Eb2 and LP. In *Bregmaceros*, he illustrates only the dorsoanterior insertion of a muscle he identified as OP, which attaches to Pb3 anteromedially. We suspect that this may equate to our M. SO-Pb3.

M. Pb2-Eb2 is commonly present in paracanthopterygians.

RANICIPITIDAE

Raniceps raninus (Linnaeus), USNM 345222, 105 mm S; USNM 307233, 105 mm.

Plate 66

Description.

LE1 on Eb1 dorsoanteriorly lateral to tip of uncinat process.

Remarks. Ligament extends medially from cartilaginous tip of uncinat process to dorsolateralmost cartilaginous edge of Pb2. Another ligament extends posterolaterally from cartilaginous tip of uncinat process to anterior edge of Eb2 anterior to lateralmost end of TEb2, and is here joined by a third ligament

extending directly posterior from the posterior edge of Eb1 posterior to LE1 insertion.

LE2 on raised bony dorsal edge of Eb2 posteriorly about mid-laterally.

LE3 absent.

LE4 massive, on most of Eb4 bony surface dorso-posteriorly lateral to uncinat process.

LP very small, easily removed or overlooked; joining LE4 insertion about mid-anteriorly.

LI1 clasps edge of Pb3 between two anterior cartilage-tipped processes (strut 1 and strut 2 of Markle, 1989:fig. 2B), dorsally ventral to OD4 origin and ventrally dorsal to Pb2.

LI2 on Pb3 posterolaterally just anterior to articulation with Eb4 and ventral to anteriorly extending SO muscle strap, which passes ventral to Eb4 portion of TPb3-Eb3-Eb4.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 broad, bandana-like, attaching broadly mid-ventrally to CT of pharyngeal roof, extending laterally and attaching to Eb2 dorsally anterior to LE2 insertion, continuing broadly posteriorly as TPb3-Eb3-Eb4. Individual sections of TPb3-Eb3-Eb4 relatively distinct and well separated laterally, but obscured from view by OD4, which lies dorsal to them: Pb3 section broadly dorsally on Pb3 process articulating with Eb2 medial end, separated by LI2 from Eb3 section, which attaches to dorsomedial bony surface of Eb3 and is separated laterally, but adjacent posteriorly, to Eb4 section, which attaches to ventromedial edge of Eb4 uncinat process (SO fibers attach to Eb4 dorsally ventromedial to Eb4 section). Eb4 section continuous mid-posteriorly with SOD.

OD3–4 origin on Pb3 dorsomedially ventral to TEb2; insertion mainly on dorsomedial edge of Eb4 uncinat process with slight tendinous connection to uncinat process of Eb3.

OP fused laterally with Ad4 and ventromedially with SO, joined ventrolaterally to raphe (ER) with Ad5; most clearly represented by strands on bony surface of Eb4 uncinat process posteriorly and Cb5 ventrally.

Ad1–3 absent.

Ad4 fused medially with OP, ventrally joining raphe with Ad5 dorsolaterally; most clearly represented by broad attachment to Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 well medial to distal end; ventrally on Cb5 dorsodistally; dorsolateral margin outlined by raphe with Ad4 and OP, but free dorso-medially and medially.

Remarks. It is unusual in acanthomorphs for the attachment of Ad5 to be so far removed medially from the distal end of Cb4. Condition also occurs in *Opsanus* (Batrachoididae), *Lactarius* (Lactariidae), cottoids, and *Xenolepidichthys* (Grammicolepidae).

SOD broad.

RDs separated by distance less than diameter of one RD.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 tiny and cartilaginous. Pb4 and UP4 absent. IAC absent.

Batrachoidiformes

BATRACHOIDIDAE

Opsanus beta (Goode and Bean), USNM 301938, 76.3 mm.

Plate 67

Description.

LE1 on anterior surface of raised bony process on Eb1.

LE2 on anterior surface of raised bony process on Eb2.

LE3 absent.

LE4 very broadly on dorsolateral surface of Eb4. LP absent.

LI1 mainly on anterolateral edge of Pb3 with minor attachment to anterior edge of Pb2 medially.

LI2 on Pb3 dorsolaterally, immediately adjacent to medial end of Eb3.

TD comprises TEb2 and TEb3-Eb4. TEb2 broad with mid-longitudinal raphe, which gives rise to CT sheets dorsally; attached mid-ventroanteriorly to CT of pharyngeal roof; muscle extends laterally and attaches on Eb2 dorsally to point anterior to mid-point of LE2 insertion. TEb3-Eb4 begins on dorsoanteromedialmost edge of Eb3 and continues around to posteromedial edge, with ventroposterior fibers attaching onto Eb4 dorsomedial surface and posteromedial edge.

OD3-4 origin broadly on Pb3 dorsally with some ventral muscle strands extending from origin onto Eb3 dorsomedially, slightly overlapping TEb3-Eb4 on Eb3; minor insertion on medial edge of Eb3 uncinat process, mainly on Eb4 uncinat process medially and posteromedially, joining raphe with OP dorsally.

OP left side dorsally on Eb4 uncinat process posteriorly, joining raphe with OD3-4 on Eb4, right side dorsally (anomalously?) on Eb3 and Eb4 uncinat processes posteriorly, ventrally on Cb5 dorsally medial to distal end, ventromedially not completely separable from SO.

Remarks. PCI (removed in Plate 67B) attaches partly to distalmost end of Cb5, but its tendinous dorsoanterior edge is joined by OP ventrolaterally and it meshes with Ad5 ventrally just dorsal to distal end of Cb5.

Ad1-3 absent.

Ad4 dorsally on ventral edge of distal half of Eb4 medial to Eb4-Cb4 joint, its medialmost edge anter-

oventral to OP; ventrally dorsal edge of distal half of Cb4.

Ad5 dorsally on Cb4 well medial to distal end, meeting Ad4 ventromedially, ventrally on Cb5 distally, its posteromedial surface meshing with PCI just dorsal to Cb5.

Remarks. It is unusual for the attachment of Ad5 to be so far removed medially from the distal end of Cb4. Condition also occurs in *Raniceps* (Gadidae), *Lactarius* (Lactariidae), cottoids, and *Xenolepidichthys* (Grammicolepididae).

SOD absent.

RDs slightly separated.

Additional remarks. SCL attached mid-dorsally to posteroventral end of Bb3. TV4 free from Cb5s. Pb4 and UP4 absent. Pb2 toothed. IAC present, reduced.

Lophiiformes

CHAUNACIDAE

Chaunax pictus Lowe, USNM 187752, 73.3 mm.

Plate 68

Description.

Remarks. The anterior ends of the Pbs of *Chaunax* appear to have been rotated dorsally and the gill arches are crowded close together.

LE1 slender, on dorsal edge of Eb1 uncinat process just lateral to tip.

LE2 very broad, on dorsoanterior edge of Eb2, meeting M. Pb2-Eb2 insertion posteriorly.

LE3 absent.

LE4 stout, on most of dorsal surface of Eb4 lateral to uncinat process, insertion meeting dorsal attachment of Ad4 on one side and insertion fibers intermingling with those of Ad4 on other side in what we consider a "sling" (Stiassny and Jensen, 1987); muscle fibers of left side twist clockwise toward origin, those of right side twist counterclockwise.

LP absent.

LI1 mainly on dorsolateralmost edge of Pb3, but slight attachment to distinct spongy CT pad attaching to dorsal cartilaginous tip of Pb3 and, on right side only, a few fibers attach to dorsalmost tip of Pb2; joins raphe anteroventrally with dorsoposterior edge of M. Pb3-Eb3.

LI2 on dorsoposterior surface of Pb3 lateral to base of dorsal process.

TD comprises TEb2, TPb2, and TEb4; TEb2 highly modified, fails to attach to Eb2 (unique among acanthomorphs we examined); muscle mostly ventral to TPb2, divided mid-longitudinally by broad raphe, which gives rise to thin CT sheets attaching to skull; anteromedially muscle on dorsoposterior surface of Pb2, attaching to spongy CT pad anterolateral to mid-longitudinal raphe, laterally with short converging anterolateral and posterolateral sections joining raphe

on dorsolateralmost edge of Pb2, which in turn is joined by another raphe laterally with M. Pb2-Eb2 medially. TPb2 a semicircular ribbon on each side arising anteriorly and posteriorly from mid-longitudinal raphe of TEb2, also forming raphe mid-laterally with TEb2. TEb4 on Eb4 posteriorly well medial to uncinete process and well lateral to medial end of Eb4.

M. Pb2-Eb2 originates anteriorly on Pb2 dorsolateralmost edge, there joining raphe with TEb2 laterally, and inserts on Eb2 along anterior edge of broad LE2 insertion.

OD3–4 originates broadly on Pb3 anteromedially, joining raphe dorsoposteriorly with ventrolateral edge of LI1; lateral fibers extend ventrally and insert on Eb3 dorsally well medial to uncinete process, remaining fibers attenuate posteriorly insert by fine tendon on Eb4 uncinete process just ventral to cartilage tip.

OP dorsally on Eb4 posteriorly below and slightly medial to uncinete process, ventrally on Cb5 dorsoposteriorly, ventromedially just meeting TV5.

Ad1–3 absent.

Ad4 dorsally broadly on Eb4 ventral to LE4 insertion, ventrally very broadly on Cb4 dorsal surface medial to Eb4-Cb4 joint.

Ad5 absent.

Remarks. The complete absence of Ad5 is uncommon in fishes. Even when not distinct, an indication of its fusion with OP or another muscle is usually discernible.

SOD present.

RDs adjacent.

Additional remarks. SCL absent. TV4 in two distinct parts, dorsal section a bilateral pair of muscles attaching separately to ventral surface of broad Bb cartilage plate; ventral section continuous, free from Cb5s, the two parts continuous by a fine muscle strand. A very similar TV4 is found only in *Dicrolele* (Ophidiidae), q.v. Pb4 and UP4 absent. IAC absent.

Acanthopterygii

Stephanoberyciformes

MELAMPHAIDAE

Poromitra capito Goode and Bean, USNM 258325, 96.1 mm.

Plate 69

Additional material. ② = *Scopelogadus mizolepis bispinosus* (Gilbert), USNM 356388, 81.7 mm.

Description.

LE1 on dorsoposterior edge of Eb1 distal to uncinete process.

LE2 on raised mid-dorsoposterior edge of Eb2.

LE3 on Eb3 dorsally lateral to uncinete process.

LE4 on posterodistal margin of Eb4 barely meeting LP anteriorly.

LP on Eb4 at and just posterior to LE4 insertion.

LI1 approximately mid-medially on dorsal surface of Pb2 anterior to uncinete process, smaller than LI2.

② Laterally on dorsal surface of Pb2 anterior to uncinete process.

LI2 on Pb3 dorsoposteriorly medial to medial end of Eb3, larger than LI1.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 broadly on dorsal surface of anterior arm of Pb2 anterior to uncinete process, posteromedianly dorsal to (appressed on) anterior end of TEb2, which it joins along mid-longitudinal raphe. TEb2 attaches on dorsoposterior edge of Eb2 medial to LE2 insertion. TPb2 and TEb2 are dorsal to and discontinuous from TPb3-Eb3, which is very thin, broad, sheet-like, and ventrally joins CT lining pharynx dorsally. Anteriorly, TPb3-Eb3 attaches broadly on Pb3 medially paralleling origin of OD3–4; posteriorly, TPb3-Eb3 expands laterally and attaches to dorsomedial end of Eb3. Change in muscle fiber direction demarcates separation of TPb3-Eb3 from SO, with which it is posteriorly broadly continuous; ② Eb3 muscle portion continuing posteriorly as band of crisscrossing fibers, which change abruptly posteriorly to all transverse SO fibers.

OD3–4 originates broadly along dorsolateral edge of Pb3 and inserts dorsally on joined Eb3-Eb4 uncinete processes.

OP dorsally on Eb4 between Ad4 and SO attachments to Eb4, ventrolaterally attaches to dorsal edge of gill raker contained in CT dorsal to Cb5, ventromedially forms raphe (ER) with Ad5, scarcely separable medially from SO. ② Well separable medially from SO.

Ad1–3 absent.

Ad4 dorsoposteriorly on bony and cartilaginous distal end of Eb4, attached by slender tendon ventrally to dorsal surface of Cb4 slightly anterior to inner angle formed by Eb4-Cb4 joint. ② Attached muscously to Cb4.

Ad5 narrowly, tendinously attached to distal end of Cb4; mid-dorsally more broadly attached to posteroventral surface of gill raker embedded in CT; dorsomedially joins raphe (ER) with to OP ventromedially; not separable medially from OP or SO; ventrally on Cb5 dorsolaterally, ventromedially continuous with SO. ② Attached muscously to Cb4.

SOD absent.

RDs small, widely separate, inserting on Pb3 dorsoposteriorly; broad, short, thin band of longitudinal SO fibers extends anteriorly on each side and slightly overlaps respective RD insertion. ② Inserts on cartilaginous posteromedial end of Pb3 and medial end of Eb4.

Additional remarks. SCL absent. TV4 free from Cb5s. Slender ligament (not illustrated) attaches tip of small prominence at cartilaginous medial end of Eb2 to Pb3 anterior to uncinat process; ② ligament absent. Autogenous rod-like cartilage attached to ventroposterior cartilaginous end of Bb3; ② rod-like cartilage absent. Pb4 absent, UP4 present. Pb1 with cartilage caps dorsally and ventrally. Pb2 toothed. Eb4 levator process absent. Medial end of Eb4 larger than that of Eb3.

Similar modified gill-raker noted in OP description, otherwise noted in this study to occur only in *Scomber*.

GIBBERICHTHYIDAE

Gibberichthys pumilus Parr, USNM 214207, 79.5 mm.

Plate 70

Description.

LE1, weak, on Eb1 near tip of uncinat process.

LE2 on posterodorsal edge of Eb2 somewhat proximal to mid-length.

LE3 on dorsoanterior surface of Eb3 uncinat process just dorsal to OD3–4 insertion.

LE4 on dorsodistal end of Eb4, joining LP insertion posteriorly, joining narrow raphe with Ad4 dorsally.

LP slender, on Eb4 joining LE4 insertion antero-laterally.

LI1 on Pb2 dorsoanteriorly ventral to anterior section of TPb2 (divides TPb2 into anterior and posterior sections).

LI2 on Pb3 mid-dorsoposteriorly, lateral to and meeting lateral edge of TPb3 attachment.

TD comprises TPb2 and TPb3. TPb2 on Pb2 anterior process and basal area of uncinat process, divided into anterior and posterior sections by LI1; anterior section partially overlies anterior end of posterior section; few muscle strands of anterior section attach to anterior end of right-side Pb3 and few strands of posterior section join OD3–4. TPb3 on Pb3 posterolaterally, meeting medial edge of LI2 insertion, posteriorly continuous with SOD.

OD3–4 anteriorly broadly on Pb3 anteromedially ventral to TPb2, divides at about posterior fourth of length with anterior branch attaching to Eb3 uncinat process and posterior branch attaching to Eb4 uncinat process.

OP dorsally on Eb4 posteriorly beginning just ventral to tip of uncinat process, ventrally joining raphe (ER) with Ad5 dorsally on Cb4.

Ad1–3 absent.

Ad4 dorsally on dorsodistalmost cartilaginous end of Eb4 posteriorly, joining narrow raphe with LE4 ventrally, ventrally broadly on Cb4 dorsodistally.

Ad5 dorsolaterally on Cb4, there joining raphe

(ER) with OP ventrally, posteroventrally on dorso-distal end of Cb5, joining raphe with TV5.

SOD present.

RDs separate anteriorly, united posteriorly at origin, inserting on Pb3 dorsal surface posteromedially.

Additional remarks. SCL present, attached dorso-medially to cartilaginous posteroventral tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 edentate. IAC absent. Eb4 levator process absent. PCI attaches to cleithrum by extremely long, fine tendon. Medial end of Eb4 much larger than that of Eb3 on one side, about same size on other.

STEPHANOBERYCIDAE

Stephanoberyx monae Gill, USNM 304376, 104 mm.

Plate 71

Description.

LE1 fine, on dorsal edge of Eb1 distal to uncinat process.

LE2 on dorsoposterior edge of Eb2 somewhat distal to mid-length of Eb2.

LE3 on dorsodistal edge of Eb3, inserts jointly with OD3 insertion.

LE4 on dorsodistalmost bony edge of Eb4, joined posteroventrally by raphe with dorsolateral portion of Ad4 origin, some fibers continuing across raphe.

LP slender, joining LE4 dorsoanterior to insertion, wrapping partway around LE4 and becoming slightly separate just ventral to origin.

LI1 on Pb2 mid-dorsolateral edge ventral to anterior section of TPb2.

LI2 on Pb3 dorsoposteriorly somewhat lateral to medial edge of bone; anteromedial half of insertion joins posteromedial half of edge of TPb3 attachment to Pb3 on one side, but is completely posterior to TPb3 insertion on the other side; posteromedial half of insertion borders SO fibers extending dorsoanteriorly along surface of Pb3.

TD comprises TPb2, TPb3, and TEb2. TPb2 separated laterally by LI1 insertion, anterior section attaches to Pb2 anterior arm, posterior section attaches at base of Pb2 uncinat process (on right side, fibers of posterior section continue short distance anteriorly ventral to anterior section before uniting with anterior section fibers). TEb2 attaches in CT enveloping dorsomedial end of Eb2-Pb2 joint. TPb3 passes laterally dorsal to OD4 origin, then extends deeply ventrally and attaches to Pb3 dorsal surface medial surface anterior to LI2 insertion on one side and meets anteromedial edge of LI2 insertion on the other side; ventral layer (not illustrated) of TPb3 muscle fibers passes knifelike through OD4 and attaches to Pb3 medial to attachment of lateral TPb3 attachment.

OD comprises OD3, OD3', OD4. OD3 and OD3' originate together on dorsoanterior surface of Pb3 beginning just posterior to cartilaginous anterior end,

muscle forms two short divisions posteriorly; lateral division inserts with LE3 insertion on Eb3 dorsodistal edge; medial division ventral surface attaches to Eb4 dorsal edge, but dorsal fibers continue without interruption posteroventrally, becoming fused with posteromedial fibers of OP (we have observed a somewhat similar condition only in *Hypoptychus*, Hypoptychidae). OD3' branches off ventral surface of OD3 shortly posterior to origin and inserts on dorsal edge of Eb3 ventral to OD3. OD4 originates on dorsal surface of Pb3 just posterior to OD3-OD3' origin and ventral to TPb3; on one side, muscle-fibers from ventral surface of TPb3 pass through OD4 anteriorly before attaching to Pb3; OD4 muscle inserts on medial edge of Eb4 bony process, which, in most fishes, bears cartilaginous tip of uncinat process.

OP originates on Eb4, fibers are continuous dorsally with posteromedial division of OD3; muscle lies posterior to Ad4 ventrolaterally; inserts ventrally on Cb4 posteriorly, joining small ER with dorsal end of Ad5.

Ad1-3 absent.

Ad4 origin on Eb4 dorsolaterally, joined by raphe with LE4 insertion, with some fibers continuous between the muscles.

Ad5 originates dorsally from raphe (ER) joining ventral end of OP on Cb4, continuous anteriorly with ventromedial OP fibers, inserting on Cb5 dorsally.

SOD present.

RDs originate together but separate before passing anteriorly ventral to SOD and TPb3; RD inserts on Pb3 dorsoposteromedial surface of Pb3, paralleling laterally adjacent SO longitudinal fibers, which also insert on Pb3 surface beginning at posterior end of OD4 origin.

Additional remarks. SCL present, attached posteromedianly by short ligament to posteroventral cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 reduced. UP4 absent; tooth plate fused to Eb3 incorrectly indicated as UP4 by Rosen (1973:472, fig. 91). Pb2 edentate. IAC absent. Eb4 levator process absent. Cartilage-tipped Eb3 and Eb4 uncinat processes absent.

BARBOURISIIDAE

Barbourisia rufa Parr, AMNH 29772, ca. 205 mm.

Plate 72

Description. Only left half of dorsal-gill arch muscles available for study.

LE1 on distal dorsal bony edge of base of Eb1 uncinat process.

LE2 on dorsalmost bony edge of Eb2.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 on Eb4 near dorsodistal end.

LP on Eb4 at and posterolateral to base of LE4.

LI1 on Pb2 dorsally, anteriorly ventral to anterior portion of TPb2.

LI2 on Pb3 dorsally.

TD comprises three parts: TPb2, TEb2, TPb3. TPb2 is divided into two portions; anterior portion on dorsal surface of Pb2 anteriorly, becoming attenuated posterolaterally, broadly continuous posteriorly with posterior portion, which attaches ventrolaterally on Pb2 medial to LI1 insertion and is posteriorly broadly continuous with TEb2 (see also remarks under SO). TEb2 attaches to Eb2 dorsally well medial to LE2 insertion and is completely separate from TPb3. TPb3 attaches dorsoposteriorly on Pb3 at joint with Eb3, and is continuously posteriorly with SOD.

OD3-4 originates ventral to TPb2 and TEb2 on Pb3 and inserts broadly on joined uncinat processes of Eb3 and Eb4.

OP represented by broad muscle attaching to Eb4 dorsoposteriorly, dorsolaterally partially continuous with LE4, attaching to Cb4 at lateral end of ER, and joining ER dorsally; broad Ad5 joins ER ventrally, possibly includes OP medially.

Ad1-3 absent.

Ad4 on Eb4 dorsoposterolaterally and Cb4 dorsally medial to internal angle of Eb4-Cb4 joint.

Ad5 broad, joining ER dorsally and Cb5 ventroposteriorly well medial to distal end; medial portion of muscle probably includes OP.

SOD present, continuous posteriorly with SO.

RDs separate, insert on dorsomedial surface of Pb3.

SO branch of transverse muscle layer arises dorsomedially from SO, curves partly around medial arc of RD, and extends anteriorly, becoming continuous with ventral surface of TPb3. Two distinct strap-like muscles originate from longitudinal layer, one attaches to Pb4 and the other to Pb3.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. Eb4 levator process absent. IAC absent.

RONDELETIIDAE

Rondeletia loricata Abe and Hotta, USNM 206836, 74.3 mm.

Plate 73

Description.

LE1 on dorsolateral bony edge of Eb1 uncinat process.

LE2 on dorsalmost bony edge of Eb2.

LE3 on tip of Eb3 uncinat process dorsal to insertion of Eb3 branch of OD3-4.

LE4 near dorsolateral end of Eb4.

LP threadlike, inserts by even finer tendon on Eb4 just distal to LE4 insertion.

LI1 on anteromedial surface of Pb2 ventral to an-

terior half of TPb2 (splits TPb2 laterally into two parts).

LI2 on posterolateral surface of Pb3, medially abutting TPb3 attachment.

TD comprises TPb2 and TPb3. TPb2 overlies OD3–4 and LI1 origins and attaches to dorsomedial surface of Pb2 anterior to Pb2 uncinate process, is divided mid-laterally by passage of LI1, and is continuous posteriorly by a few muscle strands with TPb3. TPb3 attaches to dorsolateral surface of Pb3, posteriorly abutting medial edge of LI2 insertion, and is broadly continuous posteriorly with SOD.

OD3–4 originates on Pb3 dorsoanteriorly ventral to TPb2, divides well posteriorly with short branch inserting on Eb3 uncinate process and another on Eb4 uncinate process.

OP dorsally on posterior surface of Eb4 uncinate process, in two sections; lateral section broader, ventrally on Cb5 dorsally, joining ER with Ad5 dorsally; medial section slender, medially inseparable from SO, ventrally on Cb5 dorsally posterior to Ad5 medially.

Ad1–3 absent.

Ad4 dorsally on Eb4 distal cartilaginous end, ventrally on Cb4 dorsoposterior bony surface.

Ad5 on Cb4 posteriorly well medial to distal end, joining ER with OP lateral section ventrolaterally, ventrally on distal end of Cb5 dorsodistally.

SOD present.

RDs separate, cross (right side dorsal to left side) just anterior to origins (tendinous), insert on Pb3 posteromedially.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 edentate. IAC absent, Eb4 levator process absent.

CETOMIMIDAE

Ditropichthys storeri Goode and Bean, SIO 64-24-25, 77.7 mm.

Plate 74

Description.

LE1 absent.

Remarks. *D. storeri* is the only acanthomorph we examined that lacks LE1. Another specimen should be examined to verify that the absence is not an artefact of a faulty dissection.

LE2 on Eb2 mid-dorsally.

LE3 absent.

LE4 broadly, dorsally on Eb4 just dorsomedial to OD4 insertion on Eb4.

LP filamentous, inserts by fine tendon on Eb4 at posterior margin of LE4 insertion.

LI1 on Pb2 mid-dorsally.

LI2 on Pb3 dorsal surface mid-posteriorly.

TD comprises TPb2, TEb2, TEb3, and TEb4. TPb2 band-like, dorsoanteriorly on Pb2, small ven-

trolateral slip of fibers (not visible in illustration) attaches to Pb3 lateral edge, muscle continuous posteriorly with TEb2. TEb2 string-like as it passes onto and attaches dorsally on Eb2 just medial to LE2 insertion, continuous posteriorly by fine, spaced, diagonal muscle threads with TEb3. TEb3 on Eb3 dorsomedially, forming raphe anteriorly with OD3 attachment, continuous posteriorly with TEb4. TEb4 on Eb4 anteromedial to OD4 attachment, continuous posteriorly with SOD.

OD3 and OD4 with joint origin on Pb3 dorsoanteromedial surface; unified muscle divides at point opposite mid medial edge of LI2. OD3 inserts on Eb3 anteromedially, joining raphe with TEb3. OD4 inserts on Eb4 dorsodistally at and anterior to LE4 insertion. OD4 lies mostly dorsal to OD3.

OP dorsally on Eb4 posteriorly, anteriorly overlapping most of Ad4 and possibly fusing with Ad4 posteromedially; ventrally broadly on Cb5 posterodistally.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly beginning medially anterior to much of OP (and possibly fusing with it) and extending laterally to end of Eb4, ventrally on Cb4 posterolaterally and CT joining distal ends of Cb4 and Cb5.

Ad5 apparently absent.

Remarks. It is unusual for Ad5 to be absent in acanthomorphs, and is possibly the result of the close attachment of the posterolateral surface of Cb4 and the anterolateral surface of Cb5, which obviates any function Ad5 might serve.

SOD slender, comprising loose threads of muscle.

M. SO-Pb3 strap-like section of longitudinal muscle fibers, passes anteriorly from base of diverticulum of SO and ventral to SOD, TEb3, TEb4, and OD and attaches anterolaterally to Pb3 dorsal surface.

RDs separate, vertically elliptical, insert on Pb3 dorsoposteromedially.

Additional remarks. SCL absent. TV4 complex, free from Cb5s. Pb4 tiny, UP4 large. Pb2 edentate. IAC absent. Eb3 and Eb4 uncinate processes absent. Eb4 levator process absent. Large, vertically oriented, bulb-like diverticulum on each side of SO just posterior to level of SOD; SO fibers attach to surface of diverticulum, which has two small glottis-like openings into esophagus.

Icosteiformes

ICOSTEIDAE

Icosteus aenigmaticus Lockington, LACM 35865-1, 199 mm; HSU 81-305, 188 mm.

Plate 75

Description (based primarily on LACM specimen).

LE1 shortest levator, on bony dorsal edge of Eb1 uncinate process beginning just lateral to relatively long cartilaginous medial end.

LE2 on dorsoposterior edge of bony portion of Eb2 at about mid-length and well lateral to TEb2 attachment.

LE3 on dorsoanterior surface of Eb3 uncinat process, meeting OD3–4 insertion laterally.

LE4 on bony dorsal edge of Eb4 well lateral to uncinat process.

LP on Eb4 beginning, variably, at lateral edge of LE4 insertion, or slightly anteromedial to it, and extending laterally to end of bony dorsal edge. Left-side LP anomalously doubled.

LI1 on Pb2 dorsal bony surface just posterior to anteriormost cartilage tip and on anteromedial edge of Pb3 adjacent to Pb2.

LI2 on Pb3 dorsoposteriorly medial to medial end of Eb3.

TD flat, entire dorsal surface attached to thick muscular and CT layer that lines ventral surface of skull, comprises TPb2, TEb2, and TEb3–Eb4. TPb2 kidney-shaped, concave anteriorly, attached anterolaterally to dorsal surface of Pb2 just medial to medial end of IAC; anteroventral surface attached by CT (not illustrated) to dorsoanterior surface of Pb3, CT continuing and attaching to entire posterior Pb1 surface; muscle fused ventromedially and posteriorly with TEb2, which attaches to Eb2 bony surface dorsoposteriorly just lateral to medial end and well medial to LE2 insertion. TEb2 continuous posteriorly with TEb3–Eb4, which attaches on Eb3 dorsomedially and Eb4 dorsomedial edge well medial to uncinat process, there meeting SO fibers. TEb3–Eb4 mid-posteriorly continuous by crossing muscle strands with SOD.

OD3–4 origin on Pb3 dorsally posterior to anterior cartilaginous tip, insertion on joined medial edges of Eb3 and Eb4 uncinat processes.

OP bilaterally asymmetrical (undamaged side of HSU 81-305 is like right side of LACM specimen, and is here considered to be the normal state). Right-side OP dorsally on Eb4 posteriorly, beginning lateral to uncinat process (and not clearly separate medially from SO fibers on Eb4) and extending laterally to below LE4–LP insertions, ventrally joins raphe (ER) with dorsal end of Ad5; tendon continues laterally from raphe, is joined by Ad4 ventrally, and attaches to Cb4 posterodistally. Left-side OP dorsally like right side, ventrally beginning laterally on lateral end of tendon attaching to posterolateral surface of Cb4 and extending to lateral end of Cb5; muscle not distinguishable from Ad5, if latter is present; Ad4 ventrolaterally also joins lateral end of tendon.

Remarks. The condition of OP on the right side resembles the condition in some stephanoberyci-forms, e.g., *Poromitra*, or ophidiids, e.g., *Dicrolene*, particularly in that OP is either interrupted centrally by ER or ends ventrally at ER, but in neither case does it attach to Cb5. For this reason, we record this

character as “OP wholly or partly on Cb4 and/or joining ER at level of Cb4.”

Ad1–3 absent, but fine GFM (not illustrated) on anterolateral edge of each arch.

Ad4 dorsally on Eb4 posterolaterally, beginning narrowly anteromedial to OP and extending to Eb4–Cb4 joint, ventrally on Cb4 dorsal surface medial to Eb4–Cb4 joint, with some posterolateral fibers joining tendon at ventrolateral end of OP.

Ad5 apparently, probably anomalously, absent on left side, but apparently represented by muscle strands attaching ventrally to Cb5 and dorsally joining raphe with ventral end of OP well medial to distal ends of Cb4 and Eb4. See remarks following OP.

Remarks. Attachment to ER is somewhat similar to that of *Dicrolene* (Ophidiidae) and some stephanoberyciids.

SOD broad.

RDs short, joined at origin, slightly separated anteriorly.

Additional remarks. SCL present. TV4 free from Cb5s. Tiny AC at joint between Pb1 and Eb1 on one side of LACM specimen, and on undamaged side of HSU specimen. AC between Eb1 and Cb1 and another between Eb4 and Cb4 on right side of LACM specimen; AC present between Eb4 and Cb4 on only one side of HSU specimen. Pb2 edentate; Pb3 bears only one or two fine teeth. Pb4 present. UP4 present on only one side of each specimen, each represented by a single, fine tooth. Additionally, we examined USNM 49163 (ca. 200 mm), which had gill arches preserved only on one side, and in which only UP4 had teeth (one) and LACM 32682-1 (114 mm) which had no pharyngobranchial teeth on either side.

Interrelationships (with comments on Amarsipidae and Stromateoidei). Aside from being assigned to the order Perciformes in its own suborder, Icosteoidei (e.g., J. S. Nelson, 1994), or the catchall suborder Percoidei (Weitzman, 1998), the only group the Icosteidae has been allied to is the perciform suborder Stromateoidei. The basis for a stromateoid relationship has never been explained clearly, but appears to be a general external similarity, sometimes referred to as the “stromateoid look” (Haedrich, 1967:44; Ahlstrom et al., 1976:290). Matarese et al. (1984: 577) noted that the eggs, larvae, and early juveniles of *Icosteus* superficially resemble those of stromateoid fishes, but added that more data were needed before a precise relationship could be determined. We agree that there is a remarkable general similarity in the appearance of *Icosteus*, particularly the young, and some stromateoids (compare Matarese et al., 1984:fig. 306 with Horn, 1984:fig. 333), but add that it remains to be shown that the similarities are homologs.

Haedrich (1967), who reviewed the stromateoids comprehensively (and included *Icosteus* among his

non-stromateoid comparative material), did not include *Icosteus* among possible close relatives of stromateoids. Nor did he mention *Icosteus* when he described *Amarsipus* (Haedrich, 1969), which he included among the stromateoids, even though it lacks the main stromateoid synapomorphy: saccular outgrowths posterior to the last gill arch.

Haedrich (1969) justified the inclusion of *Amarsipus* within the stromateoids by indicating a group of characters that it shares with the other stromateoids, thus implicitly re-defining the Stromateoidei: perciform caudal skeleton, uniserial jaw teeth, expanded lacrimal, inflated and protruding top of the head, extensive sub-dermal canal system, bony bridge over the anterior vertical canal of the ear, which Haedrich (1971) named the pons moultoni.

Johnson and Fritzsche (1989:16), discredited the pons moultoni as a stromateoid synapomorphy because it is widely distributed among acanthomorphs. Of the remaining characters, *Icosteus* clearly exhibits only the uniserial teeth and an inflated and protruding top of the head, both of which also occur variously among perciforms, and a perciform caudal skeleton, which is too nebulous a character to constitute a basis for relationships. The caudal fin of *Amarsipus* (Haedrich, 1969:fig. 5) is relatively unspecialized, with autogenous: parhypural, hypurals 1–5, two epurals, and two pairs of uroneurals (the plesiomorphic actinopterygian caudal fin differs in having three epurals). Also present are a short neural arch on PU2 and autogenous hemal spines on PU2 and 3. The composition of the fin, however, can vary considerably, depending on taxon, in almost every acanthomorph clade, but no percomorph has more than five hypurals.

We are uncertain of the exact structure of the caudal fin of *Icosteus* as we only had radiographs of two specimens to assess its composition. USNM 49163 and 37327: parhypural and hypurals 1 and 2 autogenous, hypurals 3, 4 and 5 (6 apparently not present) separate for most of their lengths, but all possibly fused proximally to urostyle; autogenous [paired] uroneural, two epurals, long neural spine on PU2. USNM 49163: procurent + caudal-fin rays (dorsal/ventral) 19/15, of which the central 9/9 are branched; autogenous hemal spines on PU2–6 (additionally, dorsal fin 54, of which anteriormost is a nubbin, last ray split to base; anal fin 38, of which anteriormost is a nubbin, last ray split to base; vertebrae, including caudal fin, 21+48 or 20+49). USNM 37327: procurent + caudal-fin rays 17/16 (damaged), autogenous hemal spines on PU2–4 (additionally dorsal fin 56 or 57 and anal fin 38, vertebrae 22+50). In any event, we find no basis for relating *Icosteus* with *Amarsipus* or with other stromateoids, in which the caudal fin is often more specialized than that of *Amarsipus* or *Icosteus*. We note with interest, how-

ever, the large number of autogenous hemal spines, 3 and 5 in the two specimens of *Icosteus* we radiographed. It is most unusual for acanthomorphs to have more than two autogenous hemal arches, *Stephanoberyx monae* (Stephanoberycidae), a notable exception, has 3.

We have noted no specializations of the gill-arch muscles that might indicate a close relationship between *Icosteus* and *Amarsipus* and/or the other stromateoids.

Horn (1984) compiled meristics and other characters of stromateoid taxa, including *Amarsipus*, in an attempt to unravel their intra-subordinal relationships. Using Girellidae, Kyphosidae, and Scorpididae (last now generally included in the Kyphosidae), which he considered closely related to stromateoids, as outgroups. Horn provided a cladistic analysis of the stromateoids, for which he found only three characters that supported the monophyly of *Amarsipus* + stromateoids: cycloid scales (as opposed to ctenoid), lack of scales in the preopercular area (as opposed to present), and presence of 6 hypurals (as opposed to 5). While possibly valid indications of stromateoid relations to the three outgroups, the first two characters are not particularly innovative and occur widely among percomorphs (e.g., *Icosteus* lacks scales, except for imbedded prickles along the lateral line, and on the basis of scalation cannot be excluded from relationship with stromateoids). The hypural character is erroneous. The Girellidae and Kyphosidae (including scorpidinins) have an autogenous parhypural and five autogenous hypurals, as does *Amarsipus*. Horn may have been misled by Haedrich's (1969:fig. 5) recognition of 6 hypurals in *Amarsipus*, one of which is actually the parhypural.

Without further elongating this discussion, we, like Haedrich, find no reason to ally *Icosteus* with the stromateoids. On the other hand, unlike Haedrich and more recent followers, we find no reason to consider *Amarsipus* closely related to the stromateoids. We, thus, consider the Amarsipidae to be incertae sedis among the percomorphs. (See also remarks following description of *Amarsipus*, for a possible additional character of stromateoids that is not represented in *Amarsipus*.)

Matarese et al. (1984:577) noted that the sequence of fin formation and reduced number of pelvic-fin rays in *Icosteus* are "blennioid" characters. All recently published accounts of the pelvic-fin formulae of *Icosteus* variously state that it is 4, 5, or I,4 (blennioids have I,2–I,4), but we find that there is an imbedded, greatly reduced spine closely applied to the base of the first segmented ray and that the formula is I,5 (pelvic fins are lost in the adult). We find no evidence of a relationship with the Blennioidei, or even the so-called northern blennioids, Stichaeoidei, which formerly were believed to be closely related

to the true blennioids (Springer, 1993:493). The presence of IAC and Pb2 and, occasionally, UP4 in *Icosteus* exclude it from inclusion among the Blennioidei, which possess none of these structures. The presence of a basisphenoid in *Icosteus* (R. Fritzsche, in litt., 4 Dec 2001, based on notes made by a former graduate student, K. Komori), two nostrils on each side of the head, and IAC, exclude it from inclusion among the Stichaeoidei, which lack a basisphenoid and IAC, and have a single nasal opening on each side of the head.

Of possible bearing on the relationships of the Icosteidae, are the presence of the accessory cartilages mentioned in additional remarks at the end of the muscle description of *Icosteus*. The distribution of these cartilages in acanthomorph fishes, as far as we have surveyed, is presented in Table 8. *Icosteus* has these cartilages variably at the joints between Eb1 and Cb1 and between Eb4 and Cb4 (also, uniquely in our experience, at the joint between Pb1 and Eb1). We have found these cartilages on the first or fourth arches in a variety of acanthomorphs (Table 8), but on both the first and fourth arches only in *Centropomus* (Centropomidae), *Decapterus* (Carangidae) and *Selenotoca* (Scatophagidae), besides *Icosteus* (*Decapterus* also has them on the second and third arches). For the most part, accessory cartilages are restricted to percomorphs.

Fin prickles. Another character that may have bearing on the interrelationships of *Icosteus* is the presence of fine prickles on the lateral surfaces of the rays of all fins (except for a reduced, imbedded pelvic-fin spine and a vestigial anteriormost element in the dorsal and anal fins, the fins comprise only segmented rays). Although a variety of fishes may have fin spines that are serrated or with prickles, the presence of prickles on the segmented fin rays of all or some fins is of relatively limited occurrence. Allen (2003) discusses the presence and ontogeny of the prickles in *Icosteus*. Among acanthomorphs, prickles are also present in the following (1–14):

1. Early stages of the three most specialized acanthuroid families: Luvaridae, Zancidae, and Acanthuridae (Johnson and Washington, 1987:504); thus, are synapomorphic for these families.

2. Adults of at least three tetraodontiform families (on dorsal, anal, and caudal fins), including the basal Triacanthodidae (*Tydemania navigatoris* Weber, USNM 307551; *Parahollardia lineata*) and the Balistidae (*Sufflamen chrysopterus* (Bloch and Schneider), USNM 224687, 353282; *Balistes capriscus*, USNM 240664) and Monacanthidae (*Monacanthus ciliatus* (Mitchill), USNM 353975, 353293).

3. Early juveniles (and, variously, adults) of the beryciform families Anoplogastridae, Diretmidae, Anomalopidae, and Trachichthyidae (Baldwin and Johnson, 1995; Konishi, 1999:figs. 3 & 5, provides

SEM photographs of the prickles in larval *Anomalops* and *Hoplostethus*), which together with the Monocentridae have been hypothesized to form a monophyletic Trachichthyoidei (Moore, 1993), or together with the Monocentridae, Holocentridae, and Berycidae, a monophyletic Beryciformes (Johnson and Patterson, 1993).

4. *Monocentrus japonicus* (Houttuyn) (Monocentridae; USNM 231938) has fine prickles on the segmented dorsal, anal, pectoral, and caudal fins (holocentrids do not have the prickles).

5. Segmented pelvic-fin rays of an unidentified zeiform (?Macrurocyttidae, USNM 367331).

6. *Capros aper* (Linnaeus) (Caproidae, USNM 289207), on segmented rays of all fins. *Capros* is sometimes allied to the zeiforms (Tyler et al., 2003), but was excluded from that group by Johnson and Patterson (1993) and assigned to the Perciformes. (Not present in the other caproid genus, *Antigonia*).

7. Four most specialized of the seven lampridiform families (at least dorsal fin; Olney, 1984:379; Olney et al., 1993:160): Radiicephalidae, Lophotidae, Regalecidae (*Regalecus*), Trachipteridae (*Trachipterus*, also at least caudal fin; USNM 175344; Zu, USNM 272111, also pectoral, pelvic, and caudal fins, and prickles on lateral line).

8. Stephanoberycidae, all fins (prickles also on lateral line like *Icosteus*).

9. *Barbourisia* (Barbourisidae), USNM 215469; all fins like *Icosteus*, only segmented rays (ca. 42 vert.; 21–22 dorsal-fin rays, flexible body. No IAC).

10. *Chaunax* (Chaunacidae, Lophiiformes), dorsal and caudal fins.

11. Antennariidae. According to Pietsch and Grobecker (1987:30 and table 1), spinules are present on the body and fins of most taxa. We note that the spinules may occur on the interradiial membranes as well as the segmented rays (USNM 73115).

12. Ogcocephalidae (*Dibranchius atlanticus*, USNM 158003, on base of caudal only; appears to be continuation of body armature; variably present on fins of *Ogcocephalus*). Not present in ceratioids.

13. Centriscidae (all segmented fin-rays of *Macrorhamphosus*); however this state is not present in the more specialized member of the family *Aeoliscus* (USNM 305976).

14. Priacanthidae.

To sum this up, fin prickles occur in at least some members of: Lampridiformes, Paracanthopterygii (Lophiiformes), Stephanoberyciformes, Zeiformes, Caproidae (possibly closely related to zeiforms), Beryciformes, Acanthuroidei, Tetraodontiformes, Centriscidae, and Priacanthidae.

The nature and disposition of the prickles on the fin rays and the lateral line exhibit differences among the groups. A study of the variation might indicate various interrelationships among the groups. In gen-

Table 8.—Distribution of accessory cartilages (ACs) at Eb–Cb joint of arches 1–4 in acanthomorph fishes. A few taxa that lack ACs and which are described in family accounts are included (all those not included lack ACs). * denotes taxa not mentioned in descriptive accounts. P = present; – = absent; PA = present or absent. Putatively closely related groups of families are boxed.

Taxa	AC at joint of arch				Taxa	AC at joint of arch			
	1	2	3	4		1	2	3	4
Veliferidae					Pomacanthidae				
<i>Velifer hypselopterus</i>	-	-	P	P	<i>Centropyge</i> (three species)*	-	-	-	P
<i>Metavelifer multiradiatus</i>	-	-	-	-	<i>Pomacanthodes semicirculatus</i>	-	-	-	P
Lampridae					Chaetodontidae				
<i>Lampris guttatus</i>	-	PA	-	-	<i>Chaetodon austriacus</i> *	-	-	P	-
Trachipteridae					<i>Chaetodon melannotus</i> *	-	-	P	-
<i>Trachipterus</i> sp.*	-	-	-	-	<i>Chaetodon triafasciatus</i> *	-	P	P	-
Berycidae					<i>Forcipiger flavissimus</i> *	-	P	P	-
<i>Beryx splendens</i>	-	-	-	P	<i>Heniochus acuminatus</i> *	-	-	P	-
<i>Centroberyx affinis</i>	-	-	-	P	Symphysanodontidae				
Icosteidae					<i>Symphysanodon berryi</i>	-	-	-	P
<i>Icosteus aenigmaticus</i>	PA	-	-	PA	<i>Symphysanodon octoactinus</i>	-	-	-	-
Menidae					<i>Symphysanodon</i> sp nov	-	-	-	-
<i>Mene maculata</i>	-	-	P	P	Ammodytidae				
Sebastidae					<i>Ammodytes dubius</i>	-	-	-	P
<i>Sebastes proriger</i>	-	-	-	P	Nematistiidae				
Scorpaenidae					<i>Nematistius pectoralis</i>	-	-	-	P
<i>Pontinus rathbuni</i>	-	-	-	-	Echeneidae				
<i>Neomerinthe beanorum</i>	-	-	-	-	<i>Echeneis naucrates</i>	-	-	-	P
Moronidae					<i>Remora remora</i> *	-	-	-	P
<i>Morone americana</i>	-	P	-	P	Rachycentridae				
<i>Morone mississippiensis</i>	-	-	-	P	<i>Rachycentron canadum</i>	-	-	-	P
Belonidae					Coryphaenidae				
<i>Strongylura timucu</i>	P	-	PA	?	<i>Coryphaena equiselis</i>	?	?	-	P
<i>Tylosurus crocodilus</i>	PA	-	-	?	<i>Coryphaena hippurus</i>	-	-	-	-
Scomberesocidae					Carangidae				
<i>Cololabis saira</i>	PA	-	-	-	<i>Carangoides crysos</i> *	-	-	-	P
Exocoetidae					<i>Decapterus macrosoma</i> *	P	P	P	P
<i>Exocoetus obtusirostris</i>	PA	-	-	-	<i>Decapterus punctatus</i> *	PA	PA	P	P
Hemiramphidae					<i>Selar crumenophthalmus</i>	-	-	-	P
<i>Hemiramphus far</i>	PA	P	-	-	<i>Seriola</i> sp.*	-	-	-	P
Chauliodontidae					<i>Selene vomer</i> *	-	-	-	P
<i>Chauliodus sloani</i> *	-	-	-	-	<i>Scomberoides tol</i> *	-	-	-	P
Centropomidae					Cepolidae				
<i>Centropomus undecimalis</i>	PA	-	PA	P	<i>Acanthocephala limbata</i>	-	-	-	P
Latidae					<i>Cepola rubescens</i>	-	-	-	P
<i>Lates niloticus</i>	-	-	-	P	Kuhliidae				
Ambassidae					<i>Kuhlia</i>	-	-	-	P
<i>Ambassis</i> sp.*	-	-	-	P	Arripidae				
<i>Ambassis buruensis</i>	-	-	-	-	<i>Arripis georgianus</i> *	-	-	P	P
<i>Tetracentrum caudovittatus</i>	-	-	PA	-	Terapontidae				
Dinopercidae					<i>Leiopotherapon unicolor</i>	-	-	-	P
<i>Dinoperca petersi</i> *	-	-	-	P	<i>Terapon jarbua</i>	-	-	-	-
Epigonidae					Girellidae				
<i>Epigonus pandionis</i>	-	-	-	P	<i>Girella tricuspidata</i>	-	-	-	-
<i>Sphyaenops bairdianus</i> *	-	-	-	P	Kyphosidae				
Haemulidae					<i>Kyphosus sectatrox</i> *	-	-	-	-
<i>Haemulon</i> (two species)	-	-	-	P	Scorpididae				
<i>Plectorhynchus pictus</i>	-	-	-	P	<i>Microcanthus strigatus</i> *	-	-	-	-
<i>Pomadasys crocro</i>	-	-	-	P	<i>Scorpius</i> sp.*	-	-	-	-
Inermiidae					Monodactylidae				
<i>Inermia vittata</i>	-	-	-	P	<i>Monodactylus argenteus</i> *	-	-	-	P
Lobotidae					Cichlidae				
<i>Lobotes pacificus</i>	-	-	-	P	<i>Paratilapia polleni</i>	-	PA	-	-
Coiiidae					11 other genera & species	-	-	-	-
<i>Coius</i>	-	-	-	P	Embiotocidae				
Mullidae					<i>Amphistichus argenteus</i>	-	-	-	PA
<i>Pseudupeneus maculatus</i>	-	PA	-	-	<i>Cymatogaster aggregata</i>	-	-	-	-
<i>Mulloides flavolineatus</i>	-	P	-	-	<i>Embiotoca lateralis</i>	-	-	-	P
<i>Parupeneus maculatus</i>	-	-	-	-	<i>Hysteroecarpus traskii</i>	-	-	-	-

Table 8.—Continued.

Taxa	AC at joint of arch				Taxa	AC at joint of arch			
	1	2	3	4		1	2	3	4
Percichthyidae					Embiotocidae con't				
<i>Bostockia porosa</i> *	-	-	-	-	<i>Phanerodon atripes</i>	-	-	-	P
<i>Gadopsis marmoratus</i> *	-	-	-	-	<i>Phanerodon furcatus</i>	PA	PA	-	-
<i>Macquaria colonorum</i>	-	-	-	P	<i>Rhachochilus vacca</i>	-	-	-	-
Sillaginidae					<i>Zalembeus rosaceus</i>	-	-	-	P
<i>Sillago sihama</i>	-	P	-	-	Pomacentridae				
Pempheridae					<i>Amphiprion melanopus</i>	P	PA	-	-
<i>Parapriacanthus</i>	-	-	-	P	<i>Amphiprion allardi</i>	-	-	-	-
<i>Pempheris</i>	-	-	-	P	13 other genera & 18 species	-	-	-	-
Glaucosomatidae					Labridae				
<i>Glaucosoma</i>	-	-	-	P	<i>Achoerodus viridis</i>	PA	P	P	-
Acropomatidae					<i>Bodianus mesothorax</i>	-	-	-	-
<i>Acropoma</i> sp.*	-	-	-	PA	<i>Bodianus rufus</i>	P	P	-	-
<i>Apogonops anomalus</i> *	-	-	-	P	<i>Cheilinus trilobatus</i>	-	-	-	-
<i>Doederleinia berycoides</i> *	-	-	-	P	<i>Cheilio inermis</i>	-	-	-	-
<i>Synagrops bella</i>	-	-	-	P	<i>Choerodon graphicus</i>	-	PA	-	-
Dinolestidae					<i>Choerodon cyanodus</i>	-	-	-	-
<i>Dinolestes lewini</i> *	-	-	-	-	<i>Clepticus parrae</i>	P	P	P	-
Sphyraenidae					<i>Coris julis</i>	P	P	P	-
<i>Sphyraena barracuda</i>	-	-	-	-	<i>Decodon puellaris</i>	P	PA	-	-
Gempylidae					<i>Halichoeres hortulanus</i>	PA	-	PA	-
<i>Neopinnula americana</i> *	-	-	-	-	<i>Halichoeres margaritaceus</i>	P	P	-	-
<i>Promethichthys prometheus</i> *	-	-	-	-	<i>Hologymnosus doliatus</i>	P	-	-	-
Trichiuridae					<i>Labroides dimidiatus</i>	P	P	P	-
<i>Trichiurus lepturus</i> *	-	-	-	-	<i>Notolabrus celidotus</i>	-	-	-	-
Scombridae					<i>Polylepion cruentum</i>	P	-	-	-
<i>Euthynnus alletteratus</i> *	-	-	P	P	<i>Pseudodax moluccanus</i>	-	P	P	-
<i>Scomber scombrus</i>	-	-	-	P	<i>Pseudolabrus miles</i>	P	P	-	-
<i>Scomberomorus cavalla</i> *	-	-	P	-	<i>Semicossyphus pulcher</i>	-	-	-	-
<i>Scomberomorus commersoni</i> *	-	-	P	-	<i>Suezichthys aylingi</i>	-	-	-	-
<i>Gasterochisma melampus</i> *	-	-	-	-	<i>Symphodus roissali</i>	P	-	?	-
Istiophoridae					<i>Tautoga onitis</i>	PA	PA	PA	-
<i>Istiophorus</i> sp.*	-	-	P	P	<i>Tautogolabrus adspersus</i>	-	-	-	-
Priacanthidae					Odacidae				
<i>Heteropriacanthus cruentatus</i>	-	-	-	PA	<i>Odax pullus</i>	-	-	-	-
Drepanidae					Scaridae				
<i>Drepane</i> (two species)*	-	-	-	P	<i>Leptoscarus vaigiensis</i>	-	-	-	-
Ephippidae					<i>Nicholsina denticulata</i>	-	-	-	-
<i>Chaetodipterus</i> (two species)	-	-	-	P	<i>Sparisoma aurofrenatum</i>	-	-	-	-
<i>Ephippus orbis</i> *	-	-	-	P					
<i>Platax orbicularis</i> *	PA	P	-	-	Notograptidae				
Scatophagidae					<i>Notograptus guttatus</i> *	-	-	-	-
<i>Selenotoca multifasciata</i> *	P	P	-	PA					
<i>Scatophagus argus</i> *	PA	P	-	-	Aplodactylidae				
Siganidae					<i>Crinodus lophodon</i> *	-	-	-	-
<i>Siganus (Lo) vulpinus</i> *	-	-	-	-	Centrogoniidae				
<i>Siganus (S.) spinus</i> *	-	-	-	-	<i>Centrogonys vaigiensis</i>	-	-	-	P
Acanthuridae					Leptobramidae				
<i>Acanthurus nigrofuscus</i>	-	-	-	P	<i>Leptobrama muelleri</i>	-	-	-	P

eral, prickles on the segmented fin rays are most common among deep-dwelling fishes and non-percomorphs (acanthuroids, tetraodontiforms, and priacanthids, notwithstanding).

ER, which is present in *Icosteus*, has a limited dis-

tribution among the other acanthomorphs (Table 9), and, with the possible exceptions of its presence in Menidae (*Mene*) and Centriscidae (*Macroramphosus*), ER occurs only among the more basal or non-percomorph acanthomorphs: Polymixiiformes (Poly-

Table 9.—Continued.

Taxa	Phylogenetic Inference																																												
	LE3	LP	LI1 on Pb(s)	TEb2	TEb3	TEb3-Eb4	TEb4	TPb2	TPb2a	TPb2-Pb2a-Pb3	TPb2v	TPb2-Eb2	TPb2-Pb3	TPb3	TPb3-Eb3	TPb3-Eb3-Eb4	TPb3-Eb4	TPb3-Pb4	TPb3-Pb4-Eb3	TPb3-Pb4-Eb4	TPb3-UP4	TPb3-UP4-Eb4	TPb4	TPb4-Eb3	TUP4	TUP4-Eb4	CPb	OD3	OD3'	OD4	OD4'	OD3-4	M. Pb2-Eb2	M. Pb3-Cb5	M. Pb3-UP4	Ads 1 2 3	SOD	TV4 on Cb5	SCL	ER	Eb4 flange				
Holocentridae																																													
<i>Holocentrus</i>	P	P	2	P	-	-	P	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	P	N	-	P	-		
<i>Sargocentron</i>	P	P	2	P	-	-	P	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	P	N	-	P	-		
Anomalopidae																																													
<i>Anomalops</i>	P	P	2	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	P	-		
<i>Photobalparon</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	P	-		
Centriscidae																																													
<i>Macroramphosus</i>	-	P	2	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	1 2 3	P	N	P	P	-		
Gasterosteidae																																													
<i>Gasterosteus</i>	-	P	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	-		
Hypoptychidae																																													
<i>Hypoptychus</i>	P	-	2	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	-		
<i>Aulichthys</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	-		
Aulorhynchidae																																													
<i>Aulorhynchus</i>	-	P	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	1 2 3	P	N	P	-	-		
Synbranchidae																																													
<i>Synbranchus</i>	-	-	?	P	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	-	-	P		
<i>Ophisternon</i>	PA	-	?	P	-	-	-	-	-	-	-	-	-	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	-	-	P		
Mastacembelidae																																													
<i>Mastacembelus</i>	-	-	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	-	-	-		
Elassomatidae																																													
<i>Elassoma</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	-	
Mugilidae																																													
<i>Agonostomus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	2 3	-	N	P	-	P		
Bedotiidae																																													
<i>Bedotia</i>	P	P	2	-	-	-	P	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	-	N	P	-	P		
Atherinidae																																													
<i>Menidia</i>	P	P	2	-	-	-	P	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	-	N	P	-	P		
<i>Odontesthes</i>	P	P	2	-	-	-	P	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	-	N	P	-	P	
Aplocheilidae																																													
<i>Rivulus</i>	P	P	2	-	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	1 2 3	-	Y	P	-	P	
Cyprinodontidae																																													
<i>Cyprinodon</i>	-	P	3 ^P	-	-	-	-	P	P	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	1 2 3	-	na	P	-	P	
Adrianichthyidae																																													
<i>Xenopoecilus</i>	-	P	2	-	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	2 3	-	N	P	-	P	
<i>Oryzias</i>	-	P	2	-	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	2 3	-	N	P	-	P
Belonidae																																													
<i>Tylosurus</i>	-	P	2	-	-	-	P	P	?	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	2 3	P	P	P	-	P	
<i>Strongylura</i>	-	P	2	-	-	-	-	P	?	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	2 3	P	P	P	-	P
Scomberesocidae																																													
<i>Cololabis</i>	-	P	2	-	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	2 3	P	Y	P	-	-	
Hemiramphidae																																													
<i>Hemiramphus</i>	P	P	2	-	-	-	P	P	P	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	2 3	-	Y	P	-	P	
Exocoetidae																																													
<i>Exocoetus</i>	P	P	2	-	-	-	P	P	P	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	2 3	-	Y	P	-	P
Acropomatidae																																													
<i>Synagrops</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-
Percichthyidae																																													
<i>Macquaria</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N	P	-	-
Leptobramidae																																													
<i>Leptobrama</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N	P	-	-
Latidae																																													
<i>Lates</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N	P	-	-
Centropomidae																																													
<i>Centropomus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N		

Table 9.—Continued.

Taxa	LE3	LP	LI1 on Pb(s)	TEb2	TEb3	TEb3-Eb4	TEb4	TPb2	TPb2a	TPb2-Pb2a-Pb3	TPb2v	TPb2-Eb2	TPb2-Pb3	TPb3	TPb3-Eb3	TPb3-Eb3-Eb4	TPb3-Eb4	TPb3-Pb4	TPb3-Pb4-Eb3	TPb3-Pb4-Eb4	TPb3-Pb4-Eb3-Eb4	TPb3-UP4	TPb3-UP4-Eb4	TPb4	TPb4-Eb3	TUP4	TUP4-Eb4	CPb	OD3	OD3'	OD4	OD4'	OD3-4	M. Pb2-Eb2	M. Pb3-Cb5	M. Pb3-UP4	Ads 1 2 3	SOD	TV4 on Cb5	SCL	ER	Eb4 flange				
Epigonidae																																														
<i>Epigonus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	PA	-	-	P	-	-	-	-	-	P	N	P	-	-		
Moronidae																																														
<i>Morone</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	P	-	-	-	-	P	N	P	-	-			
Serranidae																																														
<i>Epinephelus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	P	N	-	-	-			
<i>Anthias</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	P	N	-	-	-			
Lutjanidae																																														
<i>Pristipomoides</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	P	N	P	-	-			
<i>Hoplopagrus</i>	P	P	2	P	P	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	P	N	P	-	-			
Haemulidae																																														
<i>Pomadasys</i>	P	P	2 ¹	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	N	-	-	P		
<i>Haemulon</i>	P	P	2 ¹	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	N	-	-	P		
<i>Plectorhinchus</i>	P	P	2 ¹	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	N	-	-	P		
Inermiidae																																														
<i>Inermia</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	N	-	-	P		
Apogonidae																																														
<i>Glossamia</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	P	N	P	-	P	
<i>Cheilodipterus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	P	N	P	-	-	
Priacanthidae																																														
<i>Heteropriacanthus</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	N	-	-	-			
Ostracoberycidae																																														
<i>Ostracoberyx</i>	P	P	2	P	P	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-		
Cirrhitidae																																														
<i>Parracirrhites</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-		
<i>Cirrhitus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-		
Pempheridae																																														
<i>Pempheris</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-	
<i>Parapriacanthus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-	
Glaucosomatidae																																														
<i>Glaucosoma</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-	
Lactariidae																																														
<i>Lactarius</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-
Lateolabracidae																																														
<i>Lateolabrax</i>	P	P	2 ¹	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	P	N	P	-	-	
Sciaenidae																																														
<i>Cynoscion</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	-	-	-
Polynemidae																																														
<i>Polydactylus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	-	-	-
<i>Filimanus</i>	P	P	2,3	P	-	-	-	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	-	-	-
Sillaginidae																																														
<i>Sillago</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	P	P	-	-	-	-	2 3	P	N	P	-	P	
Mullidae																																														
<i>Pseudupeneus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	P	N	-	-	-
<i>Parupeneus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	P	N	-	-	-
Centrogeniidae																																														
<i>Centrogenys</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	Y	P	-	-
Ambassidae																																														
<i>Ambassis</i>	P	P	2,3	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	N	P	-	-	
<i>Tetracentrum</i>	P	P	2,3	P	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	N	P	-	P	
Caristiidae																																														
<i>Caristiis</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-
Bramidae																																														
<i>Brama</i>	-	P	2 ¹	P	-	-	-	P	-	-	-	-																																		

Table 9.—Continued.

[illegible]

Table 9.—Continued.

Taxa	LE3	LP	L1 on Pb(s)	TEb2	TEb3	TEb3-Eb4	TEb4	TPb2	TPb2a	TPb2-Pb2a-Pb3	TPb2v	TPb2-Eb2	TPb2-Pb3	TPb3	TPb3-Eb3	TPb3-Eb3-Eb4	TPb3-Eb4	TPb3-Pb4	TPb3-Pb4-Eb3	TPb3-Pb4-Eb4	TPb3-UP4	TPb3-UP4-Eb4	TPb4	TPb4-Eb3	TUP4	TUP4-Eb4	CPb	OD3	OD3'	OD4	OD4'	OD3-4	M. Pb2-Eb2	M. Pb3-Cb5	M. Pb3-UP4	Ads 1 2 3	SOD	TV4 on Cb5	SCL	ER	Eb4 flange			
<i>Dascyllus</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Lepidozygus</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Mecaenichthys</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microspathodon</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plectroglyphidodon</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pomacentrus</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Stegastes</i>	P	P	2	P	-	-	-	P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Embiotocidae																																												
<i>Amphistichus</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Embiotoca</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Cymatogaster</i>	P	P	2	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Hysteroecarpus</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Phanerodon</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Rhacochilus</i>	P	P	2	P	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Zalemnius</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Labridae																																												
<i>Achoerodus</i>	P	P	3 ^P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bodianus</i>	P	P	3 ^P	PA	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cheilinus</i>	P	P	3 ^P	P	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cheilio</i>	P	P	3 ^P	-	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Choerodon</i>	P	P	3 ^P	-	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Clepticus</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Coris</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Decodon</i>	P	P	3 ^P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Halichoeres hort.</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Halichoeres marga.</i>	P	P	3 ^P	-	-	-	-	P	P	-	-	-	-	P	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hologymnosus</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Labroides</i>	P	P	3 ^P	P	-	-	-	-	P	-	-	-	-	P	-	-	-	P	-	-	-	-	-	-	-	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Notolabrus</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polylepton</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudodax</i>	P	P	3 ^P	?	-	-	-	P	?	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudolabrus</i>	P	P	3 ^P	P	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Semicossyphus</i>	P	P	3 ^P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Suezichthys</i>	P	P	3 ^P	-	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Symphodus</i>	P	P	3 ^P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tautoga</i>	P	P	3 ^P	-	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tautogolabrus</i>	P	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xiphocheilus</i>	P	P	3 ^P	-	-	-	-	P	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odacidae																																												
<i>Odax pullus</i>	P	P	3 ^P	P	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scaridae																																												
<i>Leptoscarus</i>	P	P	3 ^P	-	-	-	-	P	?	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Nicholsina</i>	P	P	3 ^P	-	-	-	-	P	?	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sparisoma</i>	P	P	3 ^P	-	-	-	-	P	?	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pholidichthyidae																																												
<i>Pholidichthys</i>	P	P	3 ^P	-	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Luvaridae																																												
<i>Luvarus</i>	P	P	2	P	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ephippidae																																												
<i>Chaetodipterus</i>	P	P	2	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Zanclidae																																												
<i>Zanclus</i>	P	P	2	P	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-										

Table 9.—Continued.

Taxa	LE3	LP	L11 on Pb(s)	TEb2	TEb3	TEb3-Eb4	TEb4	TPb2	TPb2a	TPb2-Pb2a-Pb3	TPb2v	TPb2-Eb2	TPb2-Pb3	TPb3	TPb3-Eb3	TPb3-Eb3-Eb4	TPb3-Eb4	TPb3-Pb4	TPb3-Pb4-Eb3	TPb3-Pb4-Eb4	TPb3-UP4	TPb3-UP4-Eb4	TPb4	TPb4-Eb3	TUP4	TUP4-Eb4	CPb	OD3	OD3'	OD4	OD4'	OD3-4	M. Pb2-Eb2	M. Pb3-Cb5	M. Pb3-UP4	Ads 1 2 3	SOD	TV4 on Cb5	SCL	ER	Eb4 flange					
Channidae																																														
<i>Channa asiatica</i>	P	P	3 ^P	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	P	-	-	-	-	-	-	N	P	-	P				
<i>C. harcourtbutleri</i>	P	P	3 ^P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	P	-	-	-	-	P	-	-	-	-	-	-	N	P	-	P				
Anabantidae																																														
<i>Ctenopoma</i>	P	P	3 ^P	-	-	-	-	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	P	-	-	-	3	-	N	P	-	P						
<i>Sandelia</i>	P	P	3 ^P	-	-	-	-	P	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	P	-	-	-	2 3	-	N	P	-	P						
Amarsipidae																																														
<i>Amarsipus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	P	N	P	-	-				
Centrolophidae																																														
<i>Psenopsis</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	N	P	-	-				
Bathymasteridae																																														
<i>Bathymaster</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-			
Zaprionidae																																														
<i>Zaprora</i>	P	P	2,3	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	P	N	P	-	-			
Stichaeidae																																														
<i>Ulvaria</i>	P	P	2,3	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	1 2 3	P	N	P	-	-					
Bovichtidae																																														
<i>Bovictus</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	1 2 3	P	N	P	-	-					
Pseudaphritidae																																														
<i>Pseudaphritis</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-			
Dactylopteridae																																														
<i>Dactyloptena</i>	P	P	3 ^P	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	N	P	-	-		
Malacanthidae																																														
<i>Caulolatilus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	P	P	-	P	-	-	-	-	-	-	-	-	P	N	P	-	-			
<i>Malacanthus</i>	P	P	2	P	-	-	-	P	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	P	PA	P	-	-	-	-	-	-	-	-	P	N	P	-	-		
Draconettidae																																														
<i>Draconetta</i>	P	P	3 ^P	P	P	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	P	N	P	-	-					
Callionymidae																																														
<i>Callionymus</i>	-	P	3 ^P	P	-	-	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N	P	-	-		
Gobiesocidae																																														
<i>Trachelochismus</i>	-	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N	-	-			
Tripterygiidae																																														
<i>Ruanoho</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	-	Y	P	-	-				
<i>Lepidoblennius</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	-	Y	P	-	-				
Blenniidae																																														
<i>Parablennius gatto.</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	P	Y	P	-	-					
<i>Parablennius tasm.</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	P	Y	P	-	-					
<i>Scartella</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	?	Y	P	-	-					
<i>Scartichthys</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	P	Y	P	-	-					
<i>Istiblennius</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 2 3	P	Y	P	-	-					
Dactyloscopidae																																														
<i>Dactylagnus</i>	-	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	Y	P	-	-		
Clinidae																																														
<i>Gibbonsia</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	Y	P	-	-		
<i>Heterostichus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	Y	P	-	-	
<i>Heteroclinus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	Y	P	-	-
<i>Springeratus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Y	P	-	-
<i>Ophiclinus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	Y	P	-	-
<i>Clinus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Y	P	-	-
Labrisomidae																																														
<i>Calliclinus</i>	P	P	3 ^A	P	-	-	-	?	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Y	P	-	-	
<i>Labrisomus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Y	P	-	-	
Chaenopsidae																																														
<i>Neoclinus</i>	P	P	3 ^A	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	Y	P	-	-
Rhyacichthyidae																																														

Table 9.—Continued.

Taxa	LE3	LP	LI1 on Pb(s)	TEb2	TEb3	TEb3-Eb4	TEb4	TPb2	TPb2a	TPb2-Pb2a	TPb2-Pb2a-Pb3	TPb2v	TPb2-Eb2	TPb2-Pb3	TPb3	TPb3-Eb3	TPb3-Eb3-Eb4	TPb3-Eb4	TPb3-Pb4	TPb3-Pb4-Eb3	TPb3-Pb4-Eb4	TPb3-Pb4-Eb3-Eb4	TPb3-UP4	TPb3-UP4-Eb4	TPb4	TPb4-Eb3	TUP4	TUP4-Eb4	CPb	OD3	OD3'	OD4	OD4'	OD3-4	M. Pb2-Eb2	M. Pb3-Cb5	M. Pb3-UP4	Ads 1 2 3	SOD	TV4 on Cb5	SCL	ER	Eb4 flange				
Eleotridae																																															
<i>Eleotris</i>	P	P	2 3	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	1 2 3	P	N	P	-	P			
<i>Ophiocara</i>	P	P	2 3	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	P		
Microdesmidae																																															
<i>Ptereleotris</i>	P	P	2 3	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	P		
<i>Nemateleotris</i>	P	P	2 3	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	1 2 3	P	N	P	-	P			
<i>Microdesmus</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	-		
Gobiidae																																															
<i>Glossogobius</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	1 2 3	P	N	P	-	PA		
<i>Bollmannia</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	P	-	-	-	-	-	1 2 3	P	N	P	-	-		
<i>Padogobius</i>	P	P	2 3	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	1 2 3	P	N	P	-	P	
<i>Pseudapocryptes</i>	P	P	2	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	1 2 3	-	Y	P	-	-	
<i>Gnatholepis</i>	P	P	2 3	P	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	1 2 3	P	N	P	-	P
<i>Trypauchen</i>	P	P	2 3	P	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	1 2 3	P	N	P	-	-		
Psettodidae																																															
<i>Psettodes</i>	-	P	2	P	-	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	N	P	-	-	

mixiidae); Paracanthopterygii: Ophidiiformes (Ophidiidae, Bythitidae), Gadiformes (Ranicipitidae), Batrachoidiformes (Batrachoididae); Stephanoberyciformes (Stephanoberycidae, Gibberichthyidae, Rondeletiidae, Barbourisidae, Melamphaidae); Zeiformes (Oreosomatidae); Beryciformes (Berycidae, Anomalopidae, Holocentridae, Trachichthyidae).

Among these groups, *Icosteus*, superficially, resembles the stephanoberyciform and paracanthopterygian families (but not Stephanoberycidae), with which it variously shares to the exclusion of the other groups (data augmented from the literature): flexible body, a high number of precaudal (20–23 in *Icosteus*) and total vertebrae (67–72 in *Icosteus*), a high number of dorsal-fin rays (52–58 in *Icosteus*), attaining a length of over a meter (ca. 2 m in *Icosteus*). It also shares with these families and some cetomimid stephanoberyciforms, imbedded lateral-line scales and weakly ossified bones. It further resembles the cetomimids in lacking pelvic fins (at least as an adult), having a highly distensible stomach (also present in lophiiforms), and dorsal and anal fins consisting only of segmented rays and placed far posteriorly. It differs, at least, from all other basal acanthomorphs in having only five, as opposed to six, hypurals, and, except for some ophidiiforms and gadiforms, in having an interarcual cartilage.

The many similarities between *Icosteus* and some Stephanoberyciformes, particularly Barbourisidae, mainly favors close relationship with that group; however, the presence of IAC tends to favor the Paracanthopterygii. We assign Icosteidae to its own order, Icosteiformes, which we tentatively place near the Stephanoberyciformes, but, in any event, believe

that it occupies a pre-percomorph position among the acanthomorphs.

Zeiformes and Possible Relatives

Nelson (1994:290–291) discussed the vacillating assignments of the inter-relationships of the Caproidea through 1993: whether they are zeiforms, perciforms, a sister-group of the zeoids and tetraodontiforms, or “in some position between the Stephanoberyciformes and Beryciformes.” Nelson rejected Johnson and Patterson’s (1993) treatment of caproids as perciforms and retained them as the sister group of the zeoids (Nelson, 1994:253).

Tyler et al. (2003), conducted a phylogenetic study of the zeiforms that also included a primitive tetraodontiform (*Parahollardia*), both genera of caproids, and seven other diverse outgroups. Relationship of zeiforms with tetraodontiforms and caproids was supported in three of their four analyses (data ordered with and without most meristic characters and data unordered with most meristic characters). The relationship was not supported in the fourth analysis (data unordered without most meristic characters), which they considered, “the most rational and best justified.”

We elect to position the caproids together with the zeoids and tetraodontiforms in accordance with three of the four cladistic analyses of Tyler et al. (2003).

The presence of ER in an acanthomorph is usually an indication of a pre-percomorph condition. Only *Mene*, the centriscid *Macroramphosus*, and the enigmatic *Icosteus* (Icosteidae) among those taxa usually included in the percomorphs have it, and we present

evidence that *Icosteus* (q.v.) is more appropriately placed near the stephanobercyiforms. We also believe that *Mene*, which is generally unusual morphologically, is probably more appropriately placed among the pre-percomorphs, and have arbitrarily inserted it near the zeiforms. Although we believe that the centriscids and relatives are also probably more closely related to pre-percomorphs than to percomorphs, we place them with the other groups Johnson and Patterson (1993) included in their Smegmamorpha to facilitate discussion of that group.

Zeiformes

OREOSOMATIDAE

Allocyttus verrucosus (Gilchrist), USNM 329365, 82.8 mm.

Plate 76

Description.

Remarks. The musculature appears to be skewed atypically, but the muscles and their attachments otherwise appear normal. The muscle fibers are generally stringy and weak, particularly the posterior muscles, and are infiltrated with filmy tissue that was impossible to remove without causing considerable damage to the muscles. An anomalous muscle strap on the right side attaches to Eb1 mid-posteriorly, passes deeply ventrally, and attaches to Eb2 antero-medialmost edge.

LE1 very broadly on Eb1 dorsoposteriorly. CT covering levators laterally indents anteriorly and covers much of Eb1 posterior surface, becoming continuous with tendinous dorsal portion of LE1ventral to origin.

LE2 on Eb2 dorsoposteriorly, beginning just posterolateral to lateral end of TEb2.

LE3 absent.

LE4 dorsally on bony Eb4 process posteroventral to uncinat process, muscle joined posterolaterally by LP.

LP very fine, continuous with LE4 ventrolaterally slightly dorsal to combined insertion on Eb4.

LI1 anterior surface attaches to Pb2 posteriorly in notch between two dorsally extending cartilage-tipped processes, continues ventrally and inserts on Pb3 dorsally ventrolateral to dorsally extending cartilage-tipped process.

LI2 on Pb3 dorsolaterally ventrolateral to medial end of Eb3.

TD comprises TPb2, TEb2, TEb3, and TPb3. TPb2 very thick pad with mid-anterior U-shaped notch extending more than half distance across pad and shallow mid-posterior notch; notches joined by mid-longitudinal raphe, which gives rise to CT sheets dorsally; raphe attaches ventrally to CT of pharyngeal roof; muscle attaches anteriorly to cartilage-tipped

Pb3 dorsal and Pb2 dorsomedial processes, fuses ventrally with TEb2, and is continuous posteroventrally by muscle strand with TEb3. TEb2 attaches on Eb2 dorsally just anteromedial to LE2 insertion. TEb3 attaches to posterior margin of Eb3 medial to uncinat process. A few, probably anomalous, muscle fibers branch off right-side TEb3 and insert on Eb4 dorsally. TPb3 is a very thin ribbon of muscle (not illustrated) that extends ventroanteriorly from TEb3, where TEb3 passes dorsal to dorsoposteromedial edge of Pb3. The ribbon extends deeply ventral to OD and attaches to Pb3 dorsally in a deep depression well posterior to the anterior end of Pb3.

OD3, OD3' originate inseparably on Pb3 dorsally ventral to TEb2. OD3 inserts on Eb3 uncinat process dorsoanteriorly. OD3' branches off ventrally well lateral to origin and inserts on Eb3 dorsally anteroventral to uncinat process.

OD4 absent.

OP attaching dorsally on Eb4 posteriorly beginning medially ventral to uncinat process and extending well laterally, meeting Ad4 dorsally. A few medialmost fibers (not visible in illustration) extend ventrally to Cb5 anterior to Ad5; most fibers attach ventrally on Cb4 joining ER with Ad5, medial to distal end of Cb4, and posterior to Ad4 (ER not in view in Plate 76B).

Ad1–3 absent.

Ad4 dorsally on Eb4 mostly anterior to OP laterally, extending to near cartilaginous end of Eb4, ventrally on Cb4 dorsally beginning short distance medial to Eb4-Cb5 joint and extending to joint.

Ad5 dorsally on Cb4 well medial to distal end, ventrally on distal portion of Cb5 dorsally.

SOD absent.

RDs possibly anomalous, each divided longitudinally into two straps; right-side medial strap passes dorsal to left-side strap and lies appressed to right-side lateral strap; left-side medial strap passes medially ventral to right-side medial strap and lies appressed to medial surface of right-side lateral strap.

Additional remarks. SCL attached mid-dorsally to cartilaginous posterior tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 absent. Pb2 toothed. IAC absent. Eb1 uncinat process absent. Eb4 levator process absent.

PARAZENIDAE

Parazen pacificus Kamohara, USNM 364277, 73.0 mm; USNM 187807, 93.9 mm.

Not illustrated

ZENIONTIDAE

② = *Zenion hololepis* (Goode and Bean), USNM 187864, 68.5 mm.

Not illustrated

Description.

LE1 on Eb1 mid-dorsally (uncinate process absent), attached anteriorly for entire muscular length to perpendicular section of pharyngeal roof CT, to which Pb1 also attaches for entire length.

LE2 on Eb2 mid-dorsally.

LE3 absent on one side, much reduced, but present on other. ② Absent on both sides.

LE4 broad based, on Eb4 mid-dorsoposteriorly.

LP very fine, on Eb4 at ventrolateral edge of LE4 insertion. ② Specimen damaged, unable to determine if LP was present.

LI1 on Pb3 anteriorly near base of dorsoanterior-most process; about twice size of LI2. ② Almost entirely on Pb3, but very fine CT attachment to Pb2 present.

LI2 on Pb3 dorsolaterally anterolateral to medial end of Eb3.

TD comprises TPb2, TEb3, and TPb3. TPb2 a thick pad with broad, deep V-shaped notch (open anteriorly) leading to short mid-longitudinal raphe, which attaches dorsally to CT sheet covering muscles and ventrally to pharyngeal roof CT; muscle attaches to Pb2 and Pb3 dorsalmost surfaces posteriorly with tendinous continuation to medial edge of Pb1. TPb3 a strap of muscle extending anterolaterally ventral to OD3–4 and attaching to Pb3 along medial edge of LI2; muscle continuous mid-posteriorly with TEb3. TEb3 attaches broadly to Eb3 posterior edge, meeting OD3' posteriorly. ② Comprises TPb2, TEb2, and TEb3. TPb2 notched anteriorly and posteriorly, fused ventrally with TEb2, which attaches on Eb2 dorsoanteriorly ventral to LE2 insertion.

OD comprises OD3–4 and OD3', muscles originate on Pb3 dorsally, OD3' separating ventrally just lateral to origin; OD3–4 inserts on tip of Eb3 anteriorly, passing dorsal to tip and inserting on medial edge of Eb4; OD3' inserts on Eb3 dorsally ventral to OD3–4.

OP dorsally broadly on Eb4 posteriorly beginning near medial end and extending laterally to below lateral edge of LE4 insertion; ventrally, narrowly on Cb5 beginning dorsally on most proximal surface of long, rod-like cartilaginous distal end and extending short distance medially, meeting Ad5 medially and TV5 laterally. ② Possibly absent, but if present, attaches ventrally to Cb4 (see Ad4).

M. SO-Pb3 pair of SO longitudinal muscle straps, one on each side of each RD, extending well anteriorly and inserting on medial edge of Pb3 ventral to OD3–4. ② Absent.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly, beginning medially at lateral edge of OP and extending laterally to Eb4-Cb4 joint, ventrally broadly on Cb4 medial to joint with Eb4. ② Two layered; anterior layer typical; posterior layer, separates dorsally from anterior layer

and fuses anteroventrally with anterior layer; posterior layer possibly represents modified OP.

Ad5 triangular, apex dorsally even though muscle attaches broadly dorsally on posterior bony surface of Cb4 beginning slightly medial to cartilaginous distal end, attaches ventrally along long cartilaginous distal end of Cb5 and extends onto bony surface short distance anterior to OP. ② Cb5 cartilaginous distal end normal (short rounded cap), hence, Ad5 much less extensive ventrally.

SOD absent.

RDs separated by space more than 1.5× diameter of one RD.

Additional remarks. SCL attached mid-dorsally to cartilaginous ventroposterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 absent. Pb2 toothed. Eb4 levator process absent.

GRAMMICOLEPIDAE

Xenolepidichthys dalgleishi Gilchrist, USNM 341954, 102 mm; USNM 320015, 100 mm.

Plate 77

Description.

LE1 extremely broadly on Eb1 dorsolaterally (uncinate process absent).

LE2 on dorsally expanded posterior margin of Eb2.

LE3 on Eb3 lateral to tip of uncinate process.

LE4 on Eb4 levator process dorsoanteriorly.

LP tendinously joining LE4 slightly dorsal to cartilage tip of Eb4 levator process.

LI1 tendinously on Pb2, tendon continuing onto Pb3.

LI2 on Pb3 laterally ventral to LI1.

TD comprises TPb2, TEb2, and TEb3. TPb2 a bilateral pair of thick, rope-like muscles, separated by shallow notch mid-anteriorly and joined along their medial edges to tough, deeply depressed CT sheet (conforms dorsally with parasphenoid keel); CT sheet is tightly applied posteroventrally to TEb2 dorsally. TPb2 attaches tightly anterolaterally to cartilaginous dorsal tip of Pb2 and weakly to adjacent cartilaginous dorsal tip of Pb3. TEb2 divided medianly by narrow raphe (obscured from view in illustration); TEb2 laterally on Eb2 dorsally anterior to LE2 insertion. TPb2 and TEb2 not continuous posteriorly with TEb3. TEb3 on almost entire posterior edge of Eb3 medial to uncinate process, also attached mid-ventrally by CT to CT of pharyngeal roof.

OD3, OD3' originate together on Pb3 dorsally ventral to TEb2 and divide immediately after exiting from under TEb2, with a slender dorsal branch (OD3) attaching narrowly to Eb3 uncinate process anteriorly and a slightly larger ventral branch (OD3') attaching on Eb3 dorsally ventral to uncinate process.

OD4 absent.

OP on Eb4 dorsoposteriorly beginning ventral to uncinate process and extending medially almost to medial end, laterally overlapping Ad4 medially; ventrally on Cb4 dorsally beginning well medial to distal end and extending a short distance medially, overlapping Ad4 medially and difficult to separate from Ad4. ER, to which OP usually attaches along with Ad5 when OP attaches to Cb4, apparently absent.

Ad1–3 absent.

Remarks. As SO longitudinal fibers extend anterior to the gill arches, they spread laterally and anteriorly and form a complex mesh over the roof of the oral chamber. From this mesh, a sheet of fibers (not illustrated) extends ventrolaterally toward each of the first three arches and either attaches directly or through connective tissue to the ventral edge of the epibranchial, beginning about mid-laterally, and continuing laterally and ventrally and attaching extensively to the ceratobranchial dorsal surface medial to the inner angle of the Eb-Cb joint. The appearance in each case is superficially like an Ad, but acanthomorph Ads1–3 are on the external surface of the associated Eb-Cb pair.

Ad4 attaches dorsally along much of ventral edge of Eb4 beginning medially anterior to OP and extending laterally almost to distal end of Eb4; ventrally on much of dorsal edge of Cb4 anterior to OP.

Ad5 reduced or absent. On one side of each specimen, a short muscle (almost vestigial in smaller specimen) joins Cb5 dorsodistally to Cb4 well ventral to its distal end.

SOD absent.

RDs adjacent.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 absent. Pb2 toothed IAC absent. Eb1 uncinate process absent. Eb4 levator process present.

Caproiformes

CAPROIDAE

Capros aper (Linnaeus), USNM 289207, 2 specimens, 53.2–62.5 mm; USNM 327294, 64.8 mm.

Plate 78

Description.

LE1 on dorsolateralmost bony edge of Eb1, well lateral to long uncinate process, which is attached dorsoposteriorly by fine ligament to Pb2 anterolaterally (no IAC). Thick, tendinous edge of thin CT sheet (not illustrated) covering LEs laterally, attaches along entire posterolateral margin of LE1.

LE2 on dorsolateralmost bony edge of Eb2, ventroanteriorly meeting Ad2 dorsally and ventromedially meeting TEb2 laterally.

LE3 on Eb3 uncinate process anteriorly, ventromedial edge meeting OD3 laterally.

LE4 on Eb4 dorsolateralmost bony edge well lateral to uncinate process, joining raphe posteroventrally with Ad4 dorsally (unclearly or only partially joining raphe with Ad4 in smaller specimen).

LP absent.

LI1 in depression in cartilaginous dorsalmost surface of Pb2 just posterior to anterior end.

LI2 on Pb3 dorsoanterolaterally just ventral to overlying anteromedial edge of Eb3, insertion anteroventrally proximate to bony posterior surface of Pb2.

TD comprises TEb2 and TEb3-Eb4. TEb2 with mid-longitudinal raphe, central dorsal area with tough CT pad (not illustrated) with raised convex lateral margins, which attach to expanded dorsoanterior cartilaginous caps of Pb2s; pad attached mid-ventrally to mid-longitudinal raphe; muscle laterally covers much of dorsal surface of Eb2 and attaches dorsally at ventromedial edge of LE2 and ventrally to dorsomedial edge of Ad2, variously joining raphes with each of these two muscles. TEb3-Eb4 well separated posteriorly from TEb2, attaches broadly on posterolateral edge and surface of Eb3 (ventral to OD3 and OD3'), and posteromedial edge of Eb4; muscle slightly overlaps and is continuous ventrally by fine muscle strands with SOD.

OD3, OD3' origin on Pb2 posteromedially ventral to TEb2, continuing posteriorly broadly on Pb3 dorsomedially. OD3 inserting broadly on dorsoanterior edge of Eb3 uncinate process (there meeting ventromedial edge of LE3). OD3' separating from OD3 well ventrolateral to origin and inserting on dorsoanterior surface of Eb3, meeting dorsomedial edge of Ad3.

OD4 absent.

OP on Eb4 dorsoposteriorly beginning medially near SOD and extending laterally to near uncinate process, dorsolaterally meeting TEb3-Eb4 and dorsomedial end of Ad4, ventrally on Cb5 posteriorly just medial to distal end.

M. SO-Pb3 (not illustrated), band of longitudinal SO fibers on each side extends anteriorly ventral to TD and inserts on Pb3 medially.

Ad1 broadly on anteroventral edge of Eb1 and dorsoanteromedial surface of Cb1.

Ad2 on dorsoanterolateralmost surface of Eb2, meeting LE2 ventrally and TEb2 laterally, and on dorsoanterior surface of Cb2.

Ad3 on Eb3 anterolaterally ventral to uncinate process, meeting OD3' dorsomedially and on Cb3 dorsoanteriorly.

Ad4 on Eb4 dorsoposteriorly beginning at lateral end of OP near uncinate process and extending laterally to end of Eb4; ventrally broadly on Cb4 laterally medial to Eb4-Cb4 joint, there meeting Ad5 dorsoanterolaterally.

Ad5 short, dorsally on Cb4 dorsodistally and ven-

trally on Cb5 dorsodistally, meeting OP ventrolaterally.

SOD present.

RDs separating slightly as they pass below SOD.

Additional remarks. SCL attached mid-dorsally to elongate cartilaginous ventroposterior tip of Bb3. TV4 free from Cb5s. IAC absent. Pb4 absent, UP4 present. Pb2 toothed. Eb4 levator process absent.

Antigonia rubescens (Günther)?, USNM 365941, 76.7 mm.

Not illustrated

Additional material: ② = *Antigonia capros* Lowe USNM 163521, 78.1 mm; ③ = *A. combatia* Berry and Rathjen, USNM 188045, 91.8 mm.

Description.

LE1 finely, tendinously on dorsoposterior edge of Eb1 just lateral to uncinat process.

LE2 finely, tendinously on dorsoposterior edge of Eb2 much nearer lateral than medial end.

LE3 finely, tendinously on dorsal tip of Eb3 uncinat process.

LE4 narrowly on dorsodistal end of Eb4, joined slightly dorsal to insertion by LP.

LP very fine, joined by long slender tendon to ventrolateral edge of LE4 dorsal to joint insertion on Eb4 dorsodistally.

LI1 finely, tendinously on Pb2 posteroventrally.

LI2 tendinously on Pb3 ventrolaterally just medial to cartilaginous edge articulating with medial end of Eb3.

TD comprises TEb2 and TPb3-Eb3-Eb4. Very thick CT pad mid-dorsally extends anteriorly and attaches to Pb2s dorsoanteriorly (all but obscuring their dorsal cartilaginous ends); few small ACs irregularly distributed dorsally on pad (all three species); pad attaches mid-ventroanteriorly to CT of pharyngeal roof. TEb2 continuous from one side to the other only around CT pad posteriorly; muscle otherwise attaching medially to lateral surface of CT pad and extending laterally to, or almost to, dorsodistal end of bony surface of Eb2 (well lateral to LE2 insertion). TPb3-Eb3-Eb4 transversely continuous, free from TEb2; on Pb3 dorsal surface posterolaterally ventral to OD3-OD3', continuing onto Eb3 dorsomedially and well along posterior edges of both Eb3 and Eb4; free from SOD. ② ③ TEb2 attaches to CT pad ventrolaterally so that dorsolateral edge of pad overlaps TEb2.

OD3, OD3' origin on Pb3 dorsoposteriorly, extending laterally and branching ventrally (OD3') at about level of medial end of Eb3; OD3' inserting on Eb3 dorsally ventrolateral to uncinat process; OD3 inserting on Eb3 uncinat process anteromedially. (Note: Eb3 and Eb4 uncinat processes closely bound

together. Superficially, OD3 also appears to insert on dorsomedialmost edge of Eb4 uncinat process, but processes can be readily separated and OD3 clearly inserts only on Eb3.)

OD4 absent.

OP dorsally on Eb4 posteriorly beginning near medial end and extending laterally to below uncinat process, there meeting TPb3-Eb3-Eb4 ventrolaterally; ventrally on Cb5 posterolaterally, just meeting Ad5 ventromedially.

M. SO-Pb3, short band of longitudinal SO fibers on each side extends anteriorly ventral to TD and inserts on Pb3 medially.

AD1-3 absent, reduced muscle strands (GFM1-3) on anterolateral surfaces of respective Eb and Cb.

Ad4 dorsally on Eb4 posteriorly, beginning medially at lateral edge of OP and extending laterally to distal end of Eb4; ventrally on Cb4 dorsally extending laterally to inner angle of Eb4-Cb4 joint and anterior to Ad5 attachment.

Ad5 relatively small, dorsally on cartilaginous distal end of Cb4 posteriorly, beginning at Eb4-Cb4 joint and extending ventrally to posterolateral surface of cartilaginous distal end of Cb5.

SOD variously slender to moderately broad.

RDs adjacent for much of length, narrowing, separating, and becoming tendinous anteriorly and inserting on Pb3 posteriorly.

Additional remarks. SCL attached mid-posteriorly to greatly elongated cartilaginous ventroposterior end of Bb3. TV4 free from Cb5s. IAC reduced, ball-like suspended in ligamentous tissue (Tyler et al., 2003: table 1, indicate that IAC is absent in *A. capros*, but we found it in all three species of *Antigonia* we examined). Pb4 absent. UP4 present. Pb2 toothed. Eb4 levator process absent.

Tetraodontiformes

TRIACANTHODIDAE

Parahollardia lineata (Longley), USNM 287252, 119 mm.

Plate 79

Description.

LE1 narrowly, tendinously on Eb1 dorsoposterolaterally.

LE2 narrowly, tendinously on Eb2 dorsoposterolaterally.

LE3 narrowly, on tip of Eb3 uncinat process.

LE4 muscously and tendinously on Eb4 dorso-laterally.

LP very fine, tendinously joining LE4 posteroventrally just dorsal to LE4 insertion; origin also tendinous.

Remarks. LP in tetraodontiforms (and many other fishes) is much reduced, fragile, obscured by various

tissues, and easily destroyed when peeling away surrounding tissues. Because of this, and because he was unaware of the existence of LP in fishes at that time, Winterbottom (1974a; in litt. 19 Mar 2001), in his study of tetraodontiform musculature, did not report the presence of LP in any tetraodontiform. In addition to *Parahollardia*, we found LP in *Hollardia hollardi* Poey (USNM 289328, Triacanthodidae) and *Trixiphichthys weberi* (Chaudhuri) (USNM 280329, Triacanthidae). Additionally, in *Balistes vetula* Linnaeus (USNM 349662, Balistidae), we found a long, slender muscle extending dorsoposteriorly from a raphe with LE4 somewhat dorsal to the LE4 insertion (origin of muscle not determined). This muscle may represent a modified LP, which usually joins LE4 near the LE4 insertion. Investigation of LP in tetraodontiforms may provide information bearing on the internal classification of the order.

LI1 narrowly tendinously on dorsomedialmost tip of Pb2.

LI2 by long, slender tendon on dorsal surface of cartilaginous Pb3 process that is joined laterally by medial end of Eb3.

TD complex, comprising TPb2, TEb2, and TPb3-Eb3. TPb2 a pair of laterally curving, vertically raised muscles, lying dorsal to and mostly free from broad CT mid-section of TEb2; anteriorly, each TPb2 muscle joins CT of pharyngeal roof, which gives rise dorsally to thick CT shell that lies over TPb2s (and TEb2 portions underlying TPb2s) and forms cup attaching to ventral process on skull; posteroventrally, each TPb2 joins CT, which attaches to TEb2; CT also joined by (forms tendinous mid-anterior portion of) TEb2 (mid-posteriorly, CT of TEb2 narrows considerably); muscle does not attach to Pb2. TEb2 massive, attaching to entire bony dorsal surface of Eb2; anomalous dorsoanteromedial branch of right-side TEb2 attaches finely, tendinously to anterior end of right-side TPb2. TPb3-Eb3 on Pb3 dorsally medial to medial end of Eb2 (Eb3 portion with mid-longitudinal raphe joining TPb2 and TEb2 mid-ventrally), continuing onto Eb3 dorsolaterally ventral to OD3 and meeting OD3 insertion on uncinat process, continuous ventrally by diagonal strand of muscle with SOD.

Remarks. Because of the large thick central CT section of TEb2, we treated Pb3 as dorsally mostly not covered by muscle. This area of the Pb3s forms a diarthrosis with a knob-like process on the ventral surface of the skull, which is very similar to that of pomacentrids, but not like that of labrids, cichlids, or embiotocids. The process has an irregular surface in *Parahollardia* and pomacentrids. In the other three groups, the process is divided into a bilateral pair of broad, smooth surfaces. Stiassny and Jensen (1987: 282) characterized all the "labroids" as having a similar knob-like process, but we disagree.

OD3 origin on Pb3 dorsally ventral to TEb2, insertion massively on anterior surface of Eb3 uncinat process.

OD4 absent.

OP dorsally broadly on Eb4 posteriorly beginning on or near uncinat process and extending medially almost to end of Eb4; ventrally broadly on Cb5 posteriorly, attachment tendinous laterally and joined on one side by Ad5 posterolaterally, but not on other.

GFM1-3 large fan of fine filamentous muscle fibers attach on anterior surfaces of joined distal ends of respective Eb and Cb.

Ad4 broadly dorsally on Eb4 posteriorly beginning at or near uncinat process and extending laterally almost to end of Eb4; ventrally more restricted than dorsally, on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on distal end of Cb4 posteriorly, ventrally on Cb5 dorsodistally.

SOD present, slender, entirely ventral to TPb3-Eb3.

RDs slightly separated.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Small, spherical IAC present. Pb4 absent, UP4 present. Pb2 toothed. Eb4 levator process absent.

Winterbottom (1974a) described and illustrated the branchial arch musculature of several tetraodontiforms.

Meniformes

MENIDAE

Mene maculata (Bloch and Schneider), USNM 347107, 97.7 mm, USNM 102498, 87.8 mm.

Plate 80

Description.

LE1 on broad anterior surface of Eb1 lateral to tip of uncinat process.

LE2 on mid-dorsoposterior edge of Eb2.

LE3 tendinously on tip of Eb3 uncinat process, interrupted dorsally by CT and becoming musculus again before attaching to skull.

LE4 fan-like, joins LP ventrally on common tendon, which inserts on Eb4 lateral to uncinat process. LE4 continuous dorsally with CT from which various thin muscle straps continue dorsally and attach to skull.

LP continuous ventrally on common tendon with LE4, dorsally joining extensive CT sheet, which dorsally becomes musculus; dorsal extent of musculus LP not clearly separated from PP; CT sheet continues ventrally and attaches along outer curvature of 4th and 5th arches.

LI1 on Pb2 tendinously just posterior to joint with IAC.

LI2 on Pb3 dorsoposterolaterally.

TD comprises TEb2 and TPb3-Eb3. TEb2 very short transversely, very long longitudinally, in two continuous sections: anterior section much the broader, with mid-longitudinal raphe giving rise to CT sheets that attach to cranium; anteroventrally muscle attaches by CT to anteriormost ends of Pb2s, mid-ventrolaterally attaches to IAC2 dorsoposteriorly, and posterolaterally attaches to dorsoanteromedial surface of Eb2 anterior to medial edge of LE2 insertion; posterior section attaches to posteromedial edge of Eb2. TPb3-Eb3 begins anteriorly as diagonal strap of muscle on each side, which attaches to Pb3 dorsally ventral to posterior margin of TEb2; straps cross posteriorly just as they mesh with anterior end of broad Eb3 portion of muscle, which attaches to medial edges of Eb3s.

Remarks. The diagonal muscle straps appear to derive from crossing muscle strands present in many acanthomorph TDs, and which connect the posterior end of one TD muscle with the anterior end of another TD muscle or SOD. The straps in *Mene* are so distinctive, that they possibly are not homologous with TPb3-Eb3 in other acanthomorphs.

OD3, OD3' large, columnar, originating on dorsoanteriormost end of Pb3 ventral to TEb2, dividing posteriorly as it exits from below TEb2, with ventral branch, OD3', inserting on Eb3 dorsal surface ventroanterior to insertion of OD3, which is on anterior surface of Eb3 uncinat process.

OD4 absent.

OP complex, distinctly three-parted dorsally on Eb4, less so ventrally: medial part smallest, strap-like, beginning well medial to medial end of Eb4, curving ventrolaterally around OP middle part and inserting on tendinous raphe (ER, not illustrated) at about level of Cb4; middle part originating on Eb4 just ventral to tip of uncinat process, extending ventrally, and joining ER immediately lateral to medial OP part; lateral OP part broadest, extends laterally from middle part on Eb4 to cartilaginous distal end of Eb4 and onto AC4; sub-dorsally, medial edge of lateral OP part becomes tendinous and extends to near distal end of Cb5; tendinous edge mid-posteriorly joins ER and continues ventrally as lateral edge of OP muscle attaching to Cb5. Ad5 joins tendinous OP edge ventroposteriorly.

RecD2 slender, originating on Eb2 anteromedial edge and inserting on Eb1 ventral surface just ventral to LE1, overlies CT to which gill rakers attach ventrally.

RecD3 well developed, originating on Eb3 anteroventrolaterally and inserting on Eb2 just ventral to LE2, overlies CT to which till rakers attach ventrally.

Ad1–3 absent.

Ad4 narrow, dorsally on ventrolateral surface of Eb4 fusing anteriorly with lateral OP part ventrally

(not as apparent in posterior view as presented in Plate 80C).

Ad5 (see also OP) attaches ventrally on dorsodistal edge of Cb5, dorsally it attaches muscously and tendinously to posterodistal surfaces of Cb4 and Ad4.

SOD absent.

RDs proximate.

Additional remarks. SCL weakly attached to ventrally extending cartilaginous posterior tip of Bb3. TV4 free from Cb5s. Two interarcual cartilages: anterior IAC joins Eb1 uncinat process and tiny cartilaginous process dorsally slightly posterior to anterior bony tip of Pb2; posterior IAC (IAC2) joins cartilaginous process near posterior end of Pb2 (process is subtended by posterior extension of Pb2 toothplate; neither Pb2 process is visible in Plate 80C (IAC2 unknown for any other actinopterygian taxon). AC cartilage between distal ends of Eb3 and Cb3, another between distal ends of Eb4 and Cb4. Pb4 absent, UP4 present. Pb2 toothed. Eb4 levator process absent.

Leis (1994:140–142) compared characters (none including the dorsal gill arches) of Lactariidae, Menidae, and Carangidae and suggested the possibility that the first two families are the second and first sister groups of the third. In the discussion following Gasteromorpha, below, we suggest reasons for considering Menidae as being more closely related to pre-percomorphs than to percomorphs (such as Lactariidae and Carangidae).

Beryciformes

TRACHICHTHYIDAE

Hoplostethus mediterraneus Cuvier, USNM 307273, 79.1 mm; USNM 361959, 98.0 mm.

Plate 81

Description (based almost entirely on the smaller specimen).

Remarks. LE1–LE4 becoming long tendons dorsally and coalescing into single origin on skull. LI1–LI2 muscously attached to skull.

LE1 on dorsal edge of Eb1 well lateral to tip of uncinat process.

LE2 on posterodorsal edge of Eb2 at mid-length of Eb2.

LE3 on cartilaginous tip of Eb3 uncinat process at and dorsal to OD3–4 insertion on Eb3.

LE4 on posterolateralmost surface of Eb4.

LP absent.

LI1 on medial surface of Pb2 uncinat process.

LI2 on dorsal surface of Pb3 mid-laterally.

TD comprises TPb2', TPb2, TEb2, and TPb3-Eb3. TPb2' thin, roughly triangular, sheetlike, divided mid-longitudinally, closely applied to ventral surface of thin CT sheet, which attaches to ventral surface of

skull and envelops anterior ends of Pb2s. Mid-ventroanteriorly, TPb2' muscle fibers mesh with semi-circular, pad-like TPb2, which attaches to Pb2 anterodorsally and is anteroventrally continuous with TEb2. TEb2 inserts on Eb2 dorsal surface medial to LE2 insertion. Anteroventrally, TEb2 meshes with TPb3-Eb3. TPb3-Eb3 forms raphe dorsolaterally with OD3-4 origin (forming "bun-like" mid-dorsal section), sheet of fibers continue deep ventrolaterally and attach broadly on dorsal surface of Pb3 medial to LI2 insertion, with small muscle strap attaching to dorsomedial surface of Eb3. TPb3-Eb3 is continuous posteriorly by fine muscle strand with SOD.

Remarks. TD anomalous anteriorly in larger specimen, with separate muscle below TPb2' that attaches to Pb2 on one side and Pb3 on other; TPb2' present only unilaterally.

OD3-4 massive, originates anteriorly from Pb3 anterior end (ventral to TEb2) and dorsoposteriorly at raphe with TPb3-Eb3, inserts on lateralmost dorsoanterior surface of Eb3 uncinat process and lateralmost dorsoposterior surface of Eb4, forms raphe posteroventrally with dorsal end of OP.

OP originates dorsally from raphe with OD3-4 on Eb4 (raphe occluded from view in Plate 81B), laterally continuous with Ad4, joins raphe (ER) ventrally with Ad5.

Ad1-3 absent.

Ad4 dorsally on posterolateral surface of Eb4, continuous medially with OP, forms raphe posteroventrally with Ad5 (raphe—as ER—continues medially at ventral end of OP), attaches along dorsal surface of Cb4 anteroventrally anterior to Eb4-Cb4 joint.

Ad5 mid-ventrally broadly on Cb5 distally, expanded well ventrally beyond attachment to Cb5 with tendinous attachment to cleithrum; dorsolaterally on Cb4 distally, expands medially and joins acutely angled (two-sided) raphe dorsally: with Ad4 laterally and OP medially.

SOD present.

RDs adjacent, each inserts by short tendon on posterior end of Pb3 (in larger specimen tendinous insertion is elongate, extending well external to SO).

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 absent. Pb3 toothed. IAC absent. Eb4 levator process absent.

BERYCIDAE

Beryx splendens Lowe, USNM 306134, 3 specimens, 98.0-111 mm.

Plate 82

Description.

Remarks. LE1, 2, and 4 are tendinous (not illustrated) along lateral edge of their insertions. LE1, may form a slender, separate muscle (section) originating as a long tendon, becoming muscous ven-

trally and closely paralleling the remainder of LE1, and inserting as a long tendon at and lateral to the remainder of the LE1 insertion. Because of the variability of LE1, we do not name the separate section.

LE1 origin tendinous, insertion on Eb1 uncinat process dorsoanteriorly lateral to cartilaginous tip.

LE2 on expanded bony edge of Eb2 dorsoanteriorly.

LE3 mostly on cartilaginous tip of Eb3 uncinat process, but few muscle fibers continue and insert on tightly abutting Eb4 uncinat process.

LE4 on dorsodistalmost cartilaginous edge of Eb4.

LP very slender, becoming tendinous basally and joining lateral edge of LE4 insertion.

LI1 insertion begins dorsally on medialmost edge of Pb2 uncinat process just ventral to cartilaginous tip (joined there by dorsolateral edge of TPb2), and extends anteroventrally along posterior surface of uncinat process. About same size as LI2.

LI2 on Pb3 dorsolaterally near joint with Eb3 medialmost end.

TD comprises TPb2, TEb2-Eb1, TEb2, TPb3-Eb3, and TEb4. TPb2 arises as broad strap from median raphe on dorsoanterior surface of TEb2 and attaches to anterior surface of Pb2 uncinat process just ventral to tip of process; joined by LI1 anterior edge along Pb2 uncinat process. TEb2-Eb1 arises as narrow strap from median raphe that is continuous with TEb2 median raphe, curves anterolaterally, becoming dorsal to TEb2, and attenuating as short, slender tendon that inserts in CT surrounding tips of Eb1 and Pb2 uncinat processes; continuous posteriorly by diagonal muscle strand with TPb3-Eb3. TEb2 broad, attaches to dorsal surface of proximal bony half of Eb2, with median raphe, which gives rise dorsally to tough CT pad. TPb3-Eb3 on Pb3 bony dorsal surface medial to LI2 insertion and on Eb3 posteromedialmost surface, continuous dorsomedianly with TEb4, which is on anteromedial dorsal surface of Eb4.

Remarks. Sasaki (1989:14) first reported TEb2-Eb1 in *Beryx*, although he did not assign a name to it, nor illustrate it. We note that there is a remarkable, probably superficial, resemblance of TEb2-Eb1 to the anterior branch of the TD plexus of *Acanthurus* (q.v.).

OD3-4 originates broadly along most of length of bony dorsal surface of Pb3, inserts broadly on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP broad dorsally, on Eb4 posterior surface medial to dorsal attachment of Ad4, dorsolaterally joining raphe with OD3-4, and ventrally joining ER with dorsal edge of Ad5 on Cb4, with a few medial muscle strands continuing onto Cb5.

Remarks. Raphe with OD3-4 not present on either side of one specimen.

Ad1-3 absent.

Ad4 dorsally on Eb4 posterolateral surface and ventrally on Cb4 anterior to Eb4-Cb4 joint.

Ad5 on Cb4 posterodistally and Cb5 dorsodistally, forming raphe (ER) along dorsal edge with OP, and continuous ventrolaterally with SO.

SOD present.

RDs varying from well separated, to adjacent, to overlapping, each becoming broad tendinous strap before inserting on Pb3.

Additional remarks. SCL absent. TV4 free from Cb5s. Tiny AC 4 on dorsoposterior cartilaginous end of Cb4 (additional smaller AC4, dorsal to larger one on one side of each of two specimens). UP4 present. Pb4 absent (see below). Eb4 levator process absent. Medial end of Eb4 much larger than medial end of Eb3. IAC absent. Pb1 bony with cartilage ends. Pb2 toothed.

Rosen (1973:466, fig. 84) indicated the presence of a reduced Pb4 in *B. splendens*. This element was not present in any of our three specimens (nor in the one of *Centroberyx*). Our specimens of *Beryx splendens* were collected in the Gulf of Aden, off Somalia, whereas Rosen's specimen was collected in the Gulf of Mexico, off Mississippi. It is, therefore, quite possible that there is variation in the presence of Pb4 in *Beryx* and that more than one species is involved; a revision of the genus is warranted. We did not attempt to verify Rosen's finding and for the purposes of our study, we have treated berycids as lacking Pb4.

Centroberyx affinis (Günther), USNM 176984, 93.5 mm.

Plate 83

Description.

LE1 originating as long tendon (other LEs may have tendinous component); muscle slender, on dorsolateral edge of medially projecting Eb1 uncinat process.

LE2 on tip of expanded bony edge of Eb2.

LE3 on anterior surface of cartilaginous tip of Eb3 uncinat process.

LE4 on dorsodistalmost edge of Eb4.

LP very fine, tendinously inserted at ventrodistalmost edge of LE4 insertion.

LI1 on medial surface of Pb2 uncinat process.

LI2 tendinously on Pb3 dorsolaterally; about same size as LI1.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 roughly oblong with deep notch mid-anteriorly and extensive CT pad arising dorsally from broad mid-longitudinal raphe, which completely divides TPb2 (and TEb2); muscle attachment begins anteriorly on anterior tip of Pb2 and extends posteriorly to point on anterior edge of Pb2 uncinat process; muscle is

free anterolaterally and dorsal to anteromedial portion of TEb2, but is posteromedially and ventrally continuous with TEb2. TEb2 deeply notched mid-posteriorly at continuation of mid-longitudinal raphe; another, incomplete raphe mid-dorsally amidst TEb2, which extends laterally onto dorsal surface of Eb2 to point just medial to base of spade-like process. TPb3-Eb3 free from TPb2 and TEb2, attaches laterally to dorsal surface of Pb3 medial to LI2 insertion and attachment continues posteriorly, passing dorsal to anteromedial end of Eb4, onto posteromedialmost edge of Eb3. TPb3-Eb3 is dorsoposteriorly continuous by fine muscle strand with SOD.

Remarks. The attachment of TPb3-Eb3 to Eb3 is immediately adjacent to the abutting edges of Eb3 and Eb4. We expect that other specimens might exhibit attachment to Eb4 as well. A well-developed TEb4 is present in the related *Beryx splendens*.

OD3-4 massive, originates broadly along Pb3 ventral to TPb2 and TEb2, and inserts on anterior surface of Eb3 uncinat process and tip of Eb4 uncinat process, forming raphe posterodistally with dorsal end of OP on Eb4.

OP broad dorsally, on Eb4 posterior surface medial to dorsal attachment of Ad4, dorsolaterally forming raphe with OD3-4, and ventrally joining ER with dorsal edge of Ad5 on Cb4, with a few medial muscle strands continuing onto Cb5.

Ad1-3 absent.

Ad4 dorsally on posterodistal end of Eb4, attached continuously on posterior edge of Eb4-Cb4 joint, and continuing medially short distance on Eb4.

Ad5 dorsally on posterodistal surface of Cb4, ventrally on distal end of Cb5.

SOD very fine.

RDs adjacent.

Additional remarks. SCL absent. TV4 free from Cb5s. Tiny AC4 (not visible in dorsal view) on dorsoposterior edge of distal end of Cb4. UP4 present, Pb4 absent (see discussion in Additional remarks under *Beryx*). IAC absent. Medial end of Eb4 much larger than medial end of Eb3. Pb2 toothed.

Eb4 levator process absent; however, it appears the narrow cartilaginous distal end of Eb4, which connects expanded dorsal and ventral cartilaginous bulges, could become ossified in larger specimens, thus isolating a levator process.

HOLOCENTRIDAE

Holocentrus adscencionis (Osbeck), USNM 345408, 111 mm.

Plate 84

Additional material. *Sargocentron diadema* (Lacépède), USNM 334012, 95.8 mm.

Description.

Remarks. The muscles of the two taxa are essentially the same.

LE1 broadly on anterolateral surface of expanded bony edge of Eb1.

LE2 on expanded dorsoposterior margin of Eb2.

LE3 on joined cartilaginous tip of Eb3 uncinat process and cartilaginous edge of Eb4 uncinat process, also joins raphe with OD3–4 on these processes (joined processes completely enveloped in muscle, not visible externally).

LE4 massive, dorsolaterally on Eb4 bony surface.

LP on Eb4 at and lateral to LE4 insertion; insertion continuous ventrolaterally with CT sheet attaching to fourth and fifth arches.

LI1 on Pb2 posteroventral to uncinat process.

LI2 on Pb3 dorsoposterolaterally, just anterior to medial end of Eb3, ventromedially joining raphe with lateral edge of TPb3.

TD comprises TPb2, TEb2, TPb3, and TEb4. TPb2 on Pb2 posteromedial surface, roughly circular and pad-like, dorsally with slight ventrolateral extension on each side, notched anteriorly and giving rise to CT sheet dorsally from between notch, overlies and is broadly continuous ventrally with TEb2. TEb2 dorsal to OD3–4 origin, attaching laterally on Eb2 anterior to LE2 insertion. TPb3 broad, not connected to TPb2 or TEb2, ventral to OD3–4 origin, on Pb3 beginning on medial edge of base of Pb3 uncinat process, and extending posteriorly along ventromedial edge of LI2 insertion to position medial to medial end of Eb3, continuous by diagonal muscle strand with TEb4. TEb4 on dorsomedial surface of Eb4, continuous posteriorly by diagonal muscle band with SOD.

OD3–4 origin on Pb3 dorsomedial edge ventral to TEb2, insertion broadly on anterior surface of Eb3 uncinat process and posterior surface of Eb4 uncinat process, insertion joining raphe with LE3, which is on both processes (Eb3 uncinat process has well-developed rounded cartilaginous tip; Eb4 uncinat process is horizontal with narrow cartilaginous edge).

OP dorsally on Eb4 posteriorly and medial to Ad4 attachment, joining raphe with OD3–4 (on Eb4) posteroventrolaterally, ventrally joining ER with Ad5 dorsally on Cb4.

Ad1–3 absent.

Ad4 dorsally on Eb4 lateral to OP, ventrally on Cb4 at and medial to Eb4–Cb4 joint.

Ad5 ventrally extensively on dorsal surface of Cb5, dorsally on Cb4 well medial to distal end, there joining raphe (ER) with OP ventrally.

SOD present.

RDs adjacent.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Eb4 levator process absent. Pb2 toothed.

ANOMALOPIDAE

Anomalops katoptron (Bleeker), SIO-75-466, not measured.

Plate 85

Additional material. ② = *Photoblepharon palpebratum* (Boddaert), USNM 264123, 71.2 mm.

Description.

LE1 origin by long tendon, insertion on dorsoanterior surface of Eb1 well lateral to tip of uncinat process. ② On Eb1 immediately lateral to tip of uncinat process.

Remarks. All other levators originate muscously. Right-side uncinat process is incompletely separated from medial end of Eb1.

LE2 on dorsoanterior surface of posterodorsal bony process of Eb2.

LE3 on anterior surface of Eb3 uncinat process.

LE4 on dorsodistalmost edge of Eb4, continuous at ventrolateralmost edge of insertion with weak muscle strands, representing LP, which is continuous posteriorly with CT sheet, which changes to muscle, representing PP; LE4 ventrolaterally joins raphe with Ad4 dorsolaterally.

LP represented by weak muscle strands attaching to ventrolateralmost edge of LE4 insertion and embodied in CT sheet also including PP.

LI1 on lateral surface of Pb2 uncinat process dorsoposteriorly, noticeably larger than LI2. ② On dorsal surface of Pb2 just ventral to tip of uncinat process, same size as LI2.

LI2 on Pb3 dorsoposteriorly and slightly anteroventral to dorsomedialmost edge of Eb3.

TD comprises TPb2–Eb2 and TPb3–Eb3 (see also additional remarks end of description). TPb2–Eb2 fibers complex anteriorly, attaching to medial surfaces of Pb2s anteriorly, muscle fibers “weave” into transverse muscle fibers posteriorly that insert dorsally on Eb2, slightly lateral to medial end of Eb2 and slightly medial to expanded dorsoposterior process. TPb3–Eb3 triangular, apex anteriorly between medial ends of OD3–4s, partially ventral to OD3–4 laterally, ventrolaterally attaching to Pb3 and continuing onto dorsomedialmost surface of Eb3.

② Comprises TPb2, TEb2, and TPb3–Eb3–Eb4. TPb2 on Pb2 uncinat process, meeting LI1 insertion, continuous posteriorly by diagonal muscle strap with TEb2. TEb2 on Eb2 dorsoposteriorly well medial to LE2 insertion, continuous posteriorly by diagonal muscle strap (passing ventral to OD3–4) with TPb3–Eb3–Eb4. TPb3–Eb3–Eb4 on Pb3 dorsally beginning slightly anterior to LI2 insertion and continuing along medial edge of insertion onto Eb3 dorsoposteromedially and Eb4 dorsomedially, continuous by diagonal muscle strands with SOD.

OD3–4 origin broadly on Pb3 medially ventral to

TPb2-Eb2 posteriorly, inserting on dorsomedial edge of Eb3 uncinat process and dorsoposterior edge of Eb4 uncinat process, forming partial raphe with OP dorsolaterally. ② On Pb3 medially ventral to TEb2.

OP broad strap dorsally on posterior surface of Eb4 lateral to Ad4 dorsal attachment, forming partial raphe dorsomedially with OD3–4, narrowing slightly ventrally and forming raphe (ER) with Ad5 dorso-laterally, raphe continuous laterally between Ad5 and Ad4.

Ad1–3 absent.

Ad4 dorsally on posterolateral surface of Eb4 lateral to OP dorsally, dorsoposteriorly joining raphe with LE4 ventrally, and ventroposteriorly joining ER on Cb4 with Ad5 dorsally; anterior body of Ad4 ventrally on Cb4 dorsal surface anterior to Eb4-Cb4 joint.

Ad5 ventrally broadly on Cb5 dorsodistal surface; dorsally, beginning posterodistally on Cb4, joining raphe (ER) with Ad4 ventrally and OP ventrally.

SOD present, broad.

RDs separate, adjacent.

Additional remarks. SCL present, attached dorso-medially to posteroventral cartilaginous tip of Bb3. TV4 free from Cb5s. CT pad of TD anteriorly almost completely envelops Pb1s. Pb2 uncinat process forms small, naked articulating facet (② facet absent). Pb4 and UP4 absent. IAC small. Eb4 levator process absent.

Percomorpha

Smegmamorpha

Johnson and Patterson (1993) hypothesized this group to include Mugilomorpha, Atherinomorpha, Ellassomatidae, Gasterosteiformes (comprising Gasterosteidae, Aulorhynchidae, Hypoptychidae, Pegasidae, Indostomidae, Solenostomidae, Syngnathidae, Centriscidae, Aulostomidae, Fistulariidae), Synbranchioidei, and Mastacembeloidei. The monophyly of the group, based primarily on a single synapomorphy (origin of first epineural at distal tip of a transverse parapophysis), has been controversial ever since.

We do not believe the Smegmamorpha are monophyletic (a more formal denial is provided by Springer and Orrell in the Appendix), but, for the sake of convenience, we treat the members of the group that we examined together. We partition the Smegmamorpha into three groups, Gasterosteomorpha, Atherinomorpha, and Mugilomorpha. We believe the last two groups are closely related, but not closely related to the Gasterosteomorpha. The Atherinomorpha have been strongly supported as a monophyletic group for many years and questionably allied to the Mugilomorpha. We believe the Gasterosteomorpha are possibly polyphyletic. We recognize four groups within

the Gasterosteomorpha: Centrisciformes, Gasterosteiformes, Synbranchiformes, and Ellassomatiformes.

Johnson and Springer (1997:176) implied that there is a close relationship between Ellassomatidae and Gasterosteidae. They did not follow this with a formal publication, and the matter remains unresolved.

Gasterosteomorpha

We believe Centriscidae, particularly *Macroramphosus* (*Centriscops*, *Notopogon* should also be examined), are either a monophyletic group not closely related to other gasterosteomorphs or are the sister group of the gasterosteomorphs. *Macroramphosus* is one of only three taxa (others: *Icosteus*, Icosteidae; *Mene*, Menidae) that are usually classified among the percomorphs that possess ER and may have OP ventrally attaching to Cb4, conditions otherwise known to occur among pre-acanthomorphs (commonly) and more basal acanthomorphs (i.e., polymixiids, paracanthopterygians, zeiforms, stephanoberyciforms, beryciforms). All other of *Macroramphosus*'s putatively closely related gasterosteomorphs (i.e., syngnathoids) are highly specialized and have lost many skeletal elements; their muscles are also degenerate, but if OP is present, it attaches to Cb5.

If *Macroramphosus* is validly removed from the Gasterosteomorpha and placed in a more basal acanthomorph position, the entire classification of the Gasterosteomorpha needs to be re-evaluated, which might result in positioning the entire Gasterosteomorphas among the pre-percomorphs.

Insofar as we can determine, the term Gasterosteomorpha was first used by Nakabo (2002:53, 56, 512), who recognized Johnson and Patterson's Smegmamorpha, and included under it four groups: Gasterosteomorpha, Synbranchomorpha, Mugilomorpha, Atherinomorpha. The composition within each of these four groups mentioned only Japanese forms; therefore, it is uncertain how he would have treated Ellassomatidae, although probably as a fifth group. We employ Gasterosteomorpha here to include Centrisciformes, Gasterosteiformes, Ellassomatiformes, and Synbranchiformes. Although a reconstituted Smegmamorpha (1993) might be used for the group, we find that name marginally offensive and its original composition misleading. The ICZN does not specify that priority pertains to taxa above the family-group level.

Centrisciformes

CENTRISCIDAE

Macroramphosus scolopax (Linnaeus), USNM 366546 and 158813, both 111 mm; USNM 366727, 110 mm, 177091, 126 mm.

Description.

LE1 on high, bony spike-like Eb1 process dorso-medially (cartilage-tipped Eb1 uncinat process absent); strong, ribbon-like tendon on lateral edge of muscle, separating from muscle about halfway up from insertion and originating separately on skull; fine, thread-like tendon separates from posterior edge of ribbon-like tendon and inserts in CT around dorsal end of Pb3 laterally.

LE2 tendinously on mid-dorsal edge of Eb2 and continuing tendinously posteriorly and attaching to Eb3 mid-ventroanteriorly; anteromedial edge of insertion joined by posterodistal edge of TEb2.

LE3 absent.

LE4 on Eb4 mid-dorsally lateral to uncinat process, insertion joined posteriorly by LP.

LP tendinously on Eb4, joining LE4 insertion posteriorly.

L11 on Pb2 ventroposterior to dorsal process, and ventrolateral to origin of OD3–4 on Pb2 [sic].

L12 on Pb3 dorsally medial to anterior portion of joint articulating with medial end of Eb3.

TD comprises TEb2 and TPb3-Eb3. TEb2 relatively narrow, boomerang-like (anteriorly concave), with mid-longitudinal raphe continuing posteriorly halfway or completely across TPb3-Eb3; TEb2 attaches ventroanteriorly to complex CT pad and tissues covering dorsal ends of Pb2, Pb3, and Eb3 (tissues removed in illustration); pad continuous anteriorly and mid-ventrally with CT of pharyngeal roof (limp, but tough ligament inserts on Pb2 posteromedially ventral to cartilaginous Pb2 dorsal cap and immediately medial to origin of OD3–4 portion inserting on Pb2, and also deeply on Pb2 surrounding L11 insertion medially, thus straddling Pb2 portion of OD3–4 insertion; similar ligament inserts on Pb3 dorsoposteriorly; see also *Synbranchus*, Synbranchidae, for similar ligaments); TEb2 attaches on Eb2 beginning at and medial to LE2 insertion and continuing dorsoanterolaterally almost to distal end of Eb2, there overlain anteriorly by GFM2; TEb2 continuous with Eb3 portion of TPb3-Eb3 anteriorly by diagonal muscle strands. TPb3-Eb3 broadly triangular in dorsal view, variously appearing to consist of two meshing portions that extend laterally and attach to medial edge of Eb3 uncinat process and, separately, to Eb3 dorsal surface medial to uncinat process; muscle extends anterolaterally ventral to OD3–4-OD3' and TEb2 and attaches to Pb3 dorsomedial to joint with Eb3, and is continuous posteroventrally and posteriorly with SOD.

OD3–4, OD3' with separate origins on Pb2 and Pb3; origin on Pb2 posteromedially well ventral to large dorsal cartilage cap, straddled laterally and medially by limp ligament (described in TD above); fibers extend posteriorly from Pb2, meshing ventrally with main body of muscle originating on Pb3 ventral

to TEb2; muscle divides posteriorly with ventral fibers (OD3') inserting on Eb3 anterior surface ventral to tip of uncinat process and dorsal fibers (OD3–4) inserting finely on medial edges of joined Eb3 and Eb4 uncinat processes.

OP dorsally on posterior surface of Eb4 beginning lateral to medial end and extending laterally a varying distance, but no further than ventral to LE4 insertion, there variably separable or not from Ad4 dorsally; divided at mid-level (level at Cb4) by small raphe (ER) and attaching on Cb5 medial to Ad5, variably appearing undifferentiated from Ad5 ventral to ER.

GFM1 dorsally on and covering anterior surface of Eb1 beginning a little ventral to spike-like process and extending anteroventrally most of length of Cb1.

GFM2 beginning on Eb2 dorsomedial surface and continuing laterally on dorsoanterior surface anterior to TEb2, fanning out anterolaterally from medial attachment to Eb2, thereby anteriorly covering TEb2 laterally and Eb2-Cb2 joint, tapering ventrally, and extending anteroventrally along most of anterior surface of Cb2.

GFM3 beginning on Eb3 dorsomedially and continuing laterally, fanning out anterolaterally, covering Eb3-Cb3 joint, tapering ventrally, and extending anteroventrally along distal fifth of Cb3; thin ribbon of muscle fibers splits off GFM posterodistally and attaches to Eb3-Cb3 joint anteriorly (not visible in illustration).

Ad4 dorsally on ventral and posterior surfaces of Eb4 lateral to OP, fusing with OP anterolaterally; ventrally relatively broadly on dorsolateral surface of Cb4 medial to Eb4-Cb4 joint.

Ad5 relatively deep, dorsally on posterolateralmost surfaces of Eb4 and Cb4, covering joint of these two bones, ventrally on Cb5 dorsolaterally posterior to OP.

SOD broad, continuous anteriorly with TEb3.

RDs moderate, adjacent or slightly separated.

Additional remarks. SCL attached mid-dorsally to bony posterior end of Bb3. TV4 free from Cb5s. Pb1 cartilaginous plate, Pb4 absent, UP4 present. Pb2 toothed. IAC absent. Eb4 levator process absent.

Gasterosteiformes

GASTEROSTEIDAE

Gasterosteus aculeatus Linnaeus, USNM 344603, 62.0 mm; USNM 58296, 64.6 mm.

Plate 87

Additional material (information on these taxa included for the most part only in the data matrix, Table 12, used for the cladistic analyses). *Apeltes quadracis* (Mitchill), USNM 242691, 42.2 mm; *Culea inconstans* (Kirtland), USNM 69287 41.5

mm; *Pungitius pungitius* (Linnaeus), USNM 77842, 49.8 mm; *Spinachia spinachia* (Linnaeus), USNM 23008, 138 mm, USNM 344839, 139 mm.

Description.

LE1 on Eb1 surrounding bony or cartilage tipped uncinat process (see remarks), joining raphe anteroventrally with Ad1 dorsally; fine ligament extends posteriorly from posterolateral edge of raphe to anterior edge of Eb2. See remarks following description of LE1 in *Elassoma*.

Remarks. Primitively in acanthomorphs, the anterior or medial process of Eb1 articulates with Pb1 and the uncinat process with IAC or Pb2 (articulation may be direct or ligamentous). On this basis we consider the anterior process absent in *Elassoma* and gasterosteiforms, and the process articulating with Pb2 to be the uncinat process. We interpret the occasional presence of a small cartilage tip on the expanded edge of Eb1 in *Gasterosteus*, which is completely surrounded by the insertion of LE1, as a failure of the edge to completely ossify, as opposed to treating it as the tip of the "true" uncinat process. We know of no case where an uncinat process is present and the anterior process of Eb1 articulates with Pb2.

LE2 on raised bony process on Eb2 posterolaterally, joining raphe ventromedially with lateral end of TEb2 and another ventrolaterally with posterior portion of Ad2; fine ligament extends posteriorly from lateral edge of latter raphe to anterior edge of Eb3.

LE3 absent.

LE4 broadly on Eb4 dorsoposteriorly, joining LP anteroventrally.

Remarks. Uniquely among the gasterosteids examined, *Spinachia* apparently lacks LE4. This interpretation is based on the fact that LE4 in the other gasterosteids angles dorsoanteriorly towards its origin, whereas LP is almost vertical, as well as joining Ad5 dorsally (see LP).

LP on most of Eb4 lateral to uncinat process (may extend both lateral and medial to junction with LE4 insertion), joining raphe with Ad5 dorsally, thus forming an LP-Ad5 sling; true in all gasterosteids examined.

LI1 mostly on Pb3 dorsoanteromedially dorsal to and meeting origin of OD3–4, continuing, secondarily, onto Pb2 dorsomedially.

LI2 on Pb3 dorsoposteriorly opposite medial end of Eb3.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 broad medially, narrowing considerably laterally, with mid-longitudinal raphe giving rise dorsally to CT sheets and attaching ventroanteriorly between Pb3s to CT of pharyngeal roof, extending laterally and attaching on raised bony edge of Eb2 joining raphe with medial edge of LE2 insertion (not ex-

tending laterally past medial edge of LE2 insertion); not continuous posteriorly with TPb3-Eb3-Eb4. TPb3-Eb3-Eb4 on Pb3 dorsolaterally just medial to LI2 insertion, continuing posteriorly and attaching narrowly on dorsomedialmost end of Eb3 (there joining raphe with medial end of anterior portion of Ad3), then continuing posteriorly, but well separated laterally, with attachment to Eb4 dorsally ventromedial to uncinat process; posteriorly continuous broadly with SOD.

OD3–4 origin on Pb3 broadly dorsomedially, anteriorly ventral to and joining LI1 insertion, insertion on medial edges of Eb3 and Eb4 uncinat processes.

OP dorsally beginning on Eb4 posteriorly ventral to uncinat process and extending broadly medially, ventrally on Cb5 beginning at ventrolateral edge of Ad5, medially unclearly separable from SO.

Ad1 broad, consisting of a single portion (equivalent to posterior portion of Ad2 and Ad3) extending from raphe with LE1 ventroanteriorly across Eb1-Cb1 joint to point on Cb1 anterior bony surface just ventral to joint, ventrolateral edge attaching to filaments. Present and similar in all gasterosteids examined.

Ad2 comprising two portions, posterior portion extending from raphe with LE2 ventroanteriorly across Eb2-Cb2 joint to point on Cb2 anterior bony surface just ventral to joint; anterior portion beginning on Eb2 dorsomedially and extending laterally and passing anterior to most of posterior portion, with lateral edge attaching to gill-rakers and/or gill filaments. Present and similar in all gasterosteids examined.

Ad3 comprising two portions, posterior portion attaching dorsally to anterolateral edge of Eb3 uncinat process, continuing on ligament joining Eb3 and Eb4 uncinat processes and anterodistal end of Eb4; anterior portion beginning on dorsomedial surface of Eb3, joining raphe with lateral end of TPb3-Eb3-Eb4 and extending laterally and passing anterior to most of posterior portion, with lateral edge attaching to gill-rakers and/or gill filaments. Present and similar in all gasterosteids examined.

Ad4 dorsally on Eb4 broadly ventrally, ventrally broadly on Cb4 medial to Eb4-Cb4 joint, slightly fusing dorsoposteriorly with Ad5 dorsoposteriorly; completely obscured from view posteriorly by Ad5.

Ad5 dorsally beginning on Eb4-Cb4 joint and extending broadly medially on Eb4 to edge of OP, joining raphe with LP ventroposteriorly, ventrally on Cb5 dorsolaterally, completely overlapping Ad4 posteriorly.

SOD broad continuous anteriorly with TPb3-Eb3-Eb4.

SO lateral band of fibers extends anteriorly over medial end of Eb4 and ventral to TPb3-Eb3 and inserts on Pb3 posteriorly.

RDs adjacent.

Additional remarks. SCL present, attached mid-dorsally to wedge of cartilage, which is attached to ventral surface of cartilaginous posterior end of Bb3; Hb3s attach to wedge posterolaterally. TV4 free from Cb5s. Pb1, Pb4 and UP4 absent. Eb3 and Eb4 uncinatate processes present. Eb4 levator process absent.

Anker (1974) described and illustrated the head skeleton and muscles of *Gasterosteus aculeatus*. Our findings are in essential agreement with his.

HYPOPTYCHIDAE

Johnson and Patterson (1993) removed *Aulichthys* from the Aulorhynchidae and included it in the Hypoptychidae. We agree with that action.

Hypoptychus dybowskii Steindachner, USNM 51494, ca. 85 mm; USNM 118009, 72.8 mm; UW 29655, 3 specimens, 65–67 mm.

Plate 88

Remarks. Damage occurred in every specimen during release of the levators, and extreme difficulty was encountered in resolving the limits and attachments of the more posterior (non-levator) muscles. Additionally, there appeared to be complex variation. The description and Plate 88 are a composite based on all the specimens. Every muscle described or illustrated was seen in at least two specimens.

Description.

LE1 extremely fine, posterodistally on Eb1, continuing just onto CT (not illustrated) between Eb1 and Eb2.

LE2 extremely fine, posterodistally on Eb2, continuing just onto CT (not illustrated) between Eb2 and Eb3.

LE3 finest of all levators, usually lost during dissection, on Eb3 lateral to uncinatate process, continuing just onto CT (not illustrated) between Eb3 and Eb4; expanding at origin, and joining, or nearly so, LE4 origin.

LE4 relatively large, on Eb4 dorsolaterally, joining raphe ventrolaterally with Ad5 dorsally; muscle may appear incompletely divided into lateral section, which is continuous with Ad5, and medial section, which is not; LE4 expands at origin, probably joining, or nearly so, LE3 origin.

Remarks. The LE3 and LE4 origins are posterior to those of other levators. Usually, if not always, in percomorphs, the origins of LE3 and LE4 join the origins of the other levators, none of which ever joins the origin of LP. Our recognition of the levator on Eb4 as LE4, rather than LP is based on this fact. The alternative, that LE4 is lost and the origin of LE3 has moved posteriorly and joined that of LP, seems less parsimonious.

LP absent (see remarks following LE4).

LI1 on Pb2 dorsolaterally just anterior to articulation with Eb2.

LI2 on Pb3 posterodistally just anterior to medial end of Eb3.

TD comprises TEb2 and TPb3. TEb2 boomerang-like, attached mid-ventroanteriorly to CT of pharyngeal roof, extending laterally and attaching to Eb2 dorsally anterior to LE2; uniquely, ventrolaterally finely continuous with portion of OD3–4 origin on Pb2; posteriorly meeting but not continuous with TPb3. TPb3 broad, attaching along much of Pb3 dorsal surface, continuous posteriorly with broad SOD.

OD3–4 origin on Pb2 and Pb3 dorsally ventral to TEb2 (strands from origin on Pb2 attach on Eb2 in some specimens and join with TEb2); after passing posteriorly from under TEb2, muscle joins a branch of SO that passes posteriorly broadly over Eb4 (no raphe apparent) and continues to distal end of Cb5 medial to OP. OD3–4 extends dorsally over Eb3 and Eb4 uncinatate processes (obscuring Eb4 uncinatate process and, usually, Eb3 process in dorsal view), with slight insertion on Eb3 process and main insertion on Eb4 process, and is continuous with OP medial section on Eb4 (raphe absent).

OP strap-like, dorsally on Eb4 posterior to uncinatate process, dorsomedialmost fibers continuous with OD3–4 posteromedially; ventrally, attaching to Cb5 dorsodistally near Ad5.

Ad1 on anterodistal surface of Eb1 and dorsoanteriormost surface of Cb1.

Ad2 on anterolateral bony surface of Eb2, meeting distal end of TEb2, and dorsoanteriormost surface of Cb2.

Ad3 on most of bony surface of Eb3 lateral to uncinatate process and on dorsoanteriormost surface of Cb3.

Ad4 dorsally, broadly on Eb4 posteriorly between OP and Ad5; ventrally on Cb4, extent not determined.

Ad5 a small muscle strap, ventrally on Cb5 dorsoposterodistally; dorsally on Eb4 dorsoposterodistally, there joining raphe with LE4 ventrolaterally; small anterior portion of muscle (not visible in Plate 88) attaches to posterodistal end of Cb4.

SOD very broad.

RDs slender, separated by space more than twice one RD diameter.

Additional remarks. SCL present, questionably free from Bb3, which has ventrally extending posterior end, usually indicative that SCL attaches to it. TV4 free from Cb5s. Pb4 present, Pb1 and UP4 absent. Pb2 toothed. IAC absent. Eb1 uncinatate process present, anterior process absent (see remarks following description of LE1 under *Gasterosteus* for explanation). Eb4 uncinatate process present, levator process absent.

Aulichthys japonicus Brevoort, USNM 347504, 136 mm; USNM 59789, 129 mm; USNM 71104, 2 specimens, 68.5–71.8 mm.

Plate 89

Description.

LE1 on posterior edge of Eb1 just medial to cartilaginous distal end.

LE2 on posterior edge of Eb2 just medial to cartilaginous distal end.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 short, on Eb4 dorsoanteriorly near distal end.

LP short, on Eb4 at and posterolateral to LE4 insertion.

LI1 on Pb2 dorsoanteriorly and adjacent bony surface of Pb3 anterolaterally.

LI2 on Pb3 dorsoposteriorly anterior to medial end of Eb3.

TD comprises TEb2 and TPb3. TEb2 attaches ventromedially to CT of pharyngeal roof and laterally to Eb2 dorsally medial to LE2 insertion, continuous mid-posteriorly with TPb3. TPb3 laterally passes ventral to OD3–4 and attaches to Pb3 broadly anterior to LI2 insertion; posteriorly muscle is broadly continuous with SOD; posterolaterally, anterior fibers of SO pass through and ventral to TPb3 and insert on Pb3 medially.

Remarks. SO fibers originate diffusely medial to OP and extend dorsoanteriorly, passing among anterior SOD fibers and (difficult to see) possibly through posterior TPb3 fibers and attaching to Pb3.

OD3–4 origin on Pb2 dorsally posterior to LI1 insertion and on Pb3 dorsally ventral to TEb2, insertion on Eb3 uncinat process anteriorly and medial edge of Eb4 uncinat process.

OP dorsally on Eb4 posteriorly, extending from near medial end to uncinat process, there apparently fusing completely with Ad4 medially; ventrally on Cb5 dorsodistally, partially fusing anteriorly with Ad5; medially fusing with SO.

Ad1–3, each beginning on anterior surface of respective Eb at about mid-length of Eb and extending laterally and spreading and attaching on anterior surface of Eb-Cb joint to include cartilaginous distal end of Cb; posterior surface of muscle takes twist at distal end and appears to pass posterior to itself.

Ad4 attaches dorsally to Eb4 posteriorly lateral to uncinat process and attaches ventrally to Eb4 dorsomedially, fusing medially with dorsal half of OP.

Ad5 very reduced, ventrally on Cb5 distally, posteroventrally fusing with OP, dorsally on Cb4 posterodistally.

SOD very broad.

RDs slightly separated.

Additional remarks. SCL questionably free from Bb3. TV4 free from Cb5s. Pb1, Pb4 and UP4 absent. Pb2 toothed. IAC absent. Tiny AC present on dor-

sodistal end of Eb1, apparently not homologous with AC1 as it is completely removed from Cb1. *Aulostomus* has an elongate extension of the cartilaginous distal end of Eb1, which, if budded off, would form a similar appearing AC (*Aulostomus* is unique among gasterosteiforms in having IAC). Eb4 levator process absent. Eb1 uncinat process present, anterior process absent (see remarks following description of LE1 under *Gasterosteus* for explanation).

AULORHYNCHIDAE

Aulorhynchus flavidus Gill, USNM 344688, 2 specimens, 143–144 mm SL; USNM 167915, 89.9 mm SL.

Plate 90

Description.

LE1 on Eb1 dorsoposterolaterally, insertion continuing posteriorly on CT (not illustrated) joining Eb1 to Eb2 anterodistally.

LE2 on Eb2 dorsoposterolaterally, continuing posteriorly as CT (not illustrated) joining Eb3 anteriorly.

LE3 absent.

LE4 on Eb4 dorsolaterally.

LP on Eb4 joining LE4 insertion posteriorly, joining raphe with Ad4 dorsally.

LI1 massive, on Pb2 dorsoanteromedially and Pb3 anterolateralmost edge, which abuts Pb2.

LI2 on Pb3 dorsoposteromedially anterior to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 flat, hood-like viewed dorsally; attaches finely laterally on dorsoposterior edge of Eb2 at medial edge of LE2 insertion, attaches ventrally along mid-longitudinal line to CT of pharyngeal roof; continuous posteriorly by diagonal muscle strand with TPb3-Eb3-Eb4. TPb3-Eb3-Eb4 anterolaterally on Pb3 dorsolaterally between joints with medial ends of Eb3 and Eb4, continuing posteriorly on medial ends of Eb3 and Eb4 dorsally, continuous mid-posteriorly by diagonal muscle strands with broad SOD.

OD3–4, OD3' origin on almost entire dorsomedial margin of Pb3, muscle separates into OD3–4 dorsally and OD3' ventrally on exiting posteriorly from under TEb2; OD3–4 inserts on Eb3 uncinat process anteriorly and Eb4 uncinat process medially; OD3' inserts on Eb3 dorsally ventromedial to uncinat process. See also OP below.

OP dorsally on Eb4 posteriorly beginning ventral to and between uncinat process and LP insertion and extending medially and becoming indistinguishable from SO (in one specimen slender group of muscle fibers from OD3–4 extends posteroventrally medial to Eb4 uncinat process and joins OP fibers); ventrally on Cb5 dorsodistally, apparently fusing with Ad5 medially.

Ad1 begins on dorsoanterior surface of Eb1 an-

teromedial to LE1 insertion and follows anterior edge of Eb1 laterally, attaching to anterior surfaces of Eb1 and Cb1 where they join; short branch of muscle fibers separates anteriorly from remainder of muscle at distal end of Eb1 and attaches to distalmost gill raker of dorsal arch (rakers do not follow Eb1 margin, but extend directly anteriorly from distal end of Eb1).

Remarks. Our description of the short branch of Ad1 (and also that of Ad2 and Ad3) is problematic; Plate 90 presents another interpretation, with the short branch of fibers separating posterolaterally from the remainder of the muscle.

Ad2 begins on dorsomedialmost bony surface of Eb2 ventral to TEb2 and extends laterally on anterior edge of Eb2, covering anterior surfaces of Eb2 and Cb2 where they join; short branch of muscle fibers separates anteriorly from remainder of muscle at distal end of Eb2 and extends anteriorly, diminishing shortly and becoming CT that attaches to Eb1 posteriorly. See remarks following Ad1.

Ad3 like Ad2, but involving Eb3 and Cb3. See remarks following Ad1.

Ad4 dorsally on ventral surface of Eb4 posteriorly mostly lateral to OP, ventrally on Cb5 dorsal surface posteriorly medial to Eb4-Cb4 joint.

Ad5 questionable small band of muscle joining posterodistal end of Cb4 and anterodistal end of Cb5, fused indistinguishably with OP ventrolaterally.

SOD very broad.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to ventrally extending cartilaginous posterior tip of Bb3. TV4 free from Cb5s. Pb1 and Pb4 absent, UP4 present. Pb2 toothed. IAC absent. Eb1 uncinatate process present, anterior process absent (see remarks following description of LE1 under *Gasterosteus* for explanation). Eb4 levator process absent.

Synbranchiformes

The Synbranchiformes comprise the synbranchoids and mastacembeloids. Britz (1996) last supported recognition of a monophyletic group consisting of these two suborders. The interrelationships of the Synbranchiformes are unclear.

SYNBRANCHIDAE

Synbranchus marmoratus (Bloch), USNM 311207, 2 specimens, 298–307 mm TL.

Plate 91

Additional material. ② = *Ophisternon bengalensis* McClelland, USNM 135205, ca. 350 mm TL. Not all data were available on this specimen; absence of comment should not be interpreted as agreement with description of *S. marmoratus*.

Description.

Remarks. All of the levators extend anteriorly almost horizontally parallel to mid-line axis of body. Their orientations in the illustrations have been modified variously. ② Same.

LE1 on Eb1 dorsally near distal end. Uncinate process absent. ② Same.

LE2 divided, with separate anterior insertion on Eb2 posterodistalmost edge and posterior insertion (LE2') on CT between Cb1 and Eb3 or on CT but with tendon extending posteriorly from insertion to Cb3 somewhat ventral to joint with Eb3. ② Not divided.

Remarks. In normal position LE2 and LE2' appear to be one muscle, but manipulating the muscles they easily separate basally and the separation can be continued to (or almost to) their joint origin. The condition appears to be a derivation of the state of LE2 in the related *Mastacembelus*, in which LE2 is not divisible and inserts on Eb2 dorsoposterior edge and Eb3 dorsoanterior edge.

LE3 absent (both sides of both specimens). ② Highly reduced LE3 present on only one side; for cladistic analysis, we consider LE3 absent.

LE4 on bony dorsodistal end of Eb4, divided at origin. ② Same.

LP absent. ② Same.

LI1 massive, inserting in CT attached to medial end of IAB, enveloping Pb2 (which may be vestigial or absent), and attached to or enveloping medial end of Eb2 and anterior end of Pb3 (none of the insertion points are visible in illustrations). ② Same.

LI2 on Pb3 dorsoposterolaterally opposite medial end of Eb3. ② Same.

TD with almost complete mid-longitudinal raphe, comprises TEb2, TPb3-Eb3, and TEb4 (see additional remarks for discussion of absence of TPb2). TEb2 a pair of muscles, each angled anterolaterally and attaching on respective Pb3 dorsoanteriormost end and Eb2 dorsomedially, lies dorsal to OD3–4 origin and is continuous mid-posteriorly with TPb3-Eb3. TPb3-Eb3 (see also remarks following TD description) on Pb3 dorsally along medial edge of LI2 insertion, posteriorly extending laterally and attaching on Eb3 dorsomedially, continuous narrowly mid-posteriorly with TEb4. TEb4 more-or-less triangular, attaching along posterior edge of Eb4 and ventral surface of ligament complex extending anteriorly to Pb3 and Eb4 (exact nature of ligaments unclear), muscle continuous posteriorly with SOD. ② Comprises TEb2 (not split) and TPb3-Eb3-Eb4, shallow gap present between Pb3 and Eb3, and Eb3 and Eb4 attachments.

OD3–4 originates narrowly on joint formed by anterolateral end of Pb3 and medial end of Eb2; inserts massively dorsally on dorsolateral surface of Eb4 (covering joint with Eb3 uncinatate process and anterior edge of Eb4 (lacks uncinatate process), which may

be slightly modified as a bony process or only indented) and ventrally, less extensively on Eb3 uncinat process, the tip of which may be bony or minutely cartilaginous. ② Originates on Eb2 and adjacent Pb3 and inserts similarly to *S. marmoratus*, except muscle does not cover Eb3 and Eb4 processes (Eb3 uncinat process with cartilaginous tip).

OP dorsally on Eb4 ventrolaterally, ventrally on Cb5 dorsoposteriorly, there overlapping Ad5 ventroposteromedially, medially mostly inseparable from SO.

Ad1 (not illustrated) questionably interpreted as a fan of muscle on Eb1-Cb1 joint anteriorly; mainly associated with gill filaments.

Ad2 on Eb2 mid-dorsoanteriorly, extending ventrolaterally onto anterolateral surface of Cb2, ventral edge attached to gill filaments.

Ad3 on Eb3 anterolaterally, extending onto Cb3 anterolaterally, ventral edge attached to gill filaments.

Ad4 dorsally on Eb4 and ventrally on Cb4, medial to Eb4-Cb4 joint.

Ad5 dorsally broadly on Cb4 ventrolaterally, ventrally on Cb5 dorsally, extending medially anterior to OP.

SOD broad, continuous anteriorly with TEb4. ② Present.

RDs separated by space more than one RD diameter.

Additional remarks. SCL absent; ② Same. TV4 free from Cb5s. ② Same. Pb1 and Pb4 absent. UP4 present. Eb4 levator process absent. ② Same. Small bony flange at distal bony end of Eb4 dorsally or dorsoanteriorly shields cartilage. ② Same (see Rosen and Greenwood, 1976:fig. 35, where Eb4 flange is indicated but not labeled).

Pb2 is present as an edentate bony fragment in *S. marmoratus*. Rosen and Greenwood (1976:fig. 36) illustrate a moderately well-developed, but edentate, rod-like Pb2 in the dorsal gill-arch skeleton of *S. marmoratus*, and (figs. 28–34) and as a small, edentate, plate-like bone in all seven species of *Ophisternon*; our specimen agrees.

Rosen and Greenwood (1976:7) indicated the presence of a tendon, “t-rab, tendon of M. retractores arcum branchialium,” (their rab = our RD), which they illustrated as inserting on UP4 posteriorly in various synbranchids, but not *Synbranchus*. They did not discuss the tendon, which we believe is more accurately considered as a ligament). The ligament is integral with RD ventrolaterally for the muscle’s entire length, and it remains after the muscle is digested during clearing and staining. Rosen and Greenwood also did not mention other non-muscle integrated ligaments attaching variously to Pb3 (also attaches to cleithrum), Eb3, and Eb4 in synbranchids. On one side of the specimen of *Ophisternon*, the ligaments appear to unite in a complex mesh, and we are un-

certain if our dissections of *Synbranchus* did not destroy the integrity of the ligaments (hence, their rendition in Plate 91 should be verified).

MASTACEMBELIDAE

Mastacembelus armatus (Lacepède), USNM 319465, 275 mm; USNM 343569, 300 mm.

Plate 92

Description.

LE1 on dorsoposterior edge of Eb1 and dorsoanterior edge of Eb2, meeting Ad2 anteriorly. Cartilage-tipped Eb1 uncinat process absent.

LE2 on dorsoposterior edge of Eb2 and dorsoanterior edge of Eb3, meeting Ad3 anteriorly.

LE3 absent.

LE4 on Eb4 dorsally lateral to uncinat process.

LP absent.

LI1 massive, on joined anterior ends of Eb1, Pb2, and Pb3 dorsally, meeting anteriormost edge of OD3–4 origin.

LI2 on Pb3 dorsolaterally anterior to medial end of Eb3; muscle meets lateral edge of TPb3-Eb3.

TD comprises TEb2 and TPb3-Eb3 (a few strands of TD attach to posteromedial edge of Eb4 on one side of one specimen). TEb2 strap-like with mid-longitudinal raphe attaching dorsally to CT sheets (not shown) and ventrally to CT of pharyngeal roof; muscle attaches laterally on Eb2 dorsally, meeting posteromedial edge of LE1 insertion and medialmost edge of Ad2, and is continuous mid-posteriorly by diagonal muscle straps with TPb3-Eb3. TPb3-Eb3 broadly, dorsally on Pb3 at medial edge of LI2 insertion, continuing posteriorly and attaching on posterior edge of Eb3 medial to uncinat process; continuous posteriorly by diagonal muscle strands with SOD.

OD3–4 origin on Pb3 dorsally ventral to TEb2, meeting posterior edge of LI1 insertion; muscle divides posteriorly with dorsal portion inserting on Eb4 uncinat process and ventral portion inserting on Eb3 uncinat process (including medial edges of joined processes).

OP dorsally on Eb4 posteriorly in area ventral to uncinat process, laterally overlapping Ad4 medially, ventrally on Cb5 dorsolaterally meeting Ad5 ventrally and PCI dorsally, medially not clearly separable from SO.

Ad1–3 problematically present (as GFM?). On each epibranchial dorsoanterolaterally, there is a more-or-less well-defined strip of muscle that becomes weak and finer distally as it extends ventrally along the entire anterolateral edge of the associated ceratobranchial and attaches to the gill filaments basally.

Ad4 dorsally on ventroposterior surface of lateral half of Eb4, medially overlapped by OP, ventrally on

Cb4 dorsally medial to Eb4-Cb4 joint, there joining Ad5.

Ad5 dorsally on posterolateral end of Cb4 continuing short distance medially and joining Ad4 ventrolaterally, ventrally on distal end of Cb5, there joining OP medially and PCI dorsoanteriorly.

SOD present.

SO muscle straps arise from SO in area lateral to SOD, extend anteriorly dorsal to Eb4 and attach variously to Pb4, Eb3, or Eb4.

RDs separated by space about equal to diameter of one RD.

Additional remarks. SCL absent (Bb3 with ventroposteriorly extending cartilaginous tip). TV4 free from Cb5s. Pb1 absent. Pb2 toothed. Pb4 and UP4 present. IAC absent. Eb4 levator process absent.

Elassomatiformes

ELASSOMATIDAE

Elassoma zonatum Jordan, USNM 173343, 30.5 mm; USNM 232536, 29.9 mm.

Plate 93

Description.

LE1 on Eb1 dorsolaterally, anterior edge of insertion bordering Ad1 dorsomedially.

Remarks. Medial end of Eb1 articulates with Pb2 and we consider it to be the uncinat process. We consider the anterior Eb1 process, which articulates with Pb1, but never with Pb2, when present, is absent in *Elassoma* and the gasterosteiforms. See remarks following description of LE1 in *Gasterosteus*.

LE2 on Eb2 dorsoposterolaterally, anterior edge of insertion bordering Ad2 dorsally, medial edge bordering TEb2 posterolaterally.

LE3 on tip of Eb3 uncinat process.

LE4 on Eb4 dorsolaterally posterior to Eb3 uncinat process (Eb4 uncinat process absent).

LP on Eb4 along posterior edge of LE4 insertion, posteriorly just dorsal to Ad4 dorsally.

LI1 on anteromedial edge of Pb2 and, mainly, on adjacent anteromedial edge of Pb3 slightly anterior to OD3-4 origin.

LI2 on Pb3 dorsolaterally anteromedial to medial end of Eb3; medial edge of insertion joins lateral edge of TPb3-Eb3-Eb4.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 very wide, mid-anterior notch leading to mid-longitudinal raphe that continues across anterior half of TPb3-Eb3-Eb4; attached mid-ventrally to CT of pharyngeal roof, giving rise dorsally to CT sheets; attached laterally to Eb2 dorsally at and anterior to LE2 insertion, meeting LE2 insertion anteriorly and Ad2 attachment medially; continuous posteriorly by fine diagonal muscle filament with TPb3-Eb3-Eb4. TPb3-Eb3-Eb4 attaching to Pb3 dorsolaterally at medial

edge of LI2, continuing onto Eb3 dorsomedialmost surface and Eb4 dorsomedially; continuous posteriorly by diagonal muscle strand with SOD.

OD3-4 origin broadly on Pb3 dorsoanteromedially and adjacent edge of Pb2 ventral to TEb2; insertion on Eb3 uncinat process anteriorly and dorsal edge of Eb4 adjacent to Eb3 uncinat process.

OP dorsally on Eb4 ventroposteromedially, ventrally on Cb5 posterolaterally.

Remarks. Although we describe Ad1 and 3 as having one or two sections, we are uncertain in those cases where only one section is present whether it is the result of variation or damage in dissection. Furthermore, it is possibly more accurate to describe the Ads as having one or two shapes.

Ad1 variably with anterior and posterior sections; anterior section dorsally on anterolateral edge of Eb1, posterior section dorsally meeting anterior edge of LE1; sections fuse laterally and attach to anterior surface of distal ends of Eb1 and Cb1.

Ad2 with anterior and posterior sections; anterior section dorsally extending medially and meeting anterodistal edge of TEb2; posterior section meeting ventroanterior edge of LE2 insertion; sections fuse laterally and attach to anterior surface of distal ends of Eb2 and Cb2.

Ad3 variably with anterior and posterior sections; anterior section on anterolateral edge of laterally and attach to anterolateral surface of Eb3 and Cb3; when posterior section is absent, medial attachment is to Eb3 ventroanterior to uncinat process.

Ad4 dorsally on Eb4 posteriorly ventral to LP insertion and lateral to OP; ventrally on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 posterolaterally, ventrally on Cb5 dorsolaterally.

SOD broad, continuous anteriorly with TPb3-Eb3-Eb4.

RDs slightly separated.

Additional remarks. SCL attached mid-dorsally to ventral surface of cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb1 and Pb4 absent, UP4 present. Pb2 toothed. IAC absent. Eb4 levator process absent.

Mugilomorphpha

MUGILIDAE

Agonostomus monticola (Bancroft), USNM 322336, 90.4 mm, USNM 372452, 110 mm (gill arches now cleared and stained).

Plate 94

Description.

LE1 narrowly on cartilaginous tip of Eb1 uncinat process.

LE2 on tip of dorsally expanded bony posterior

edge of Eb2; ligament extends from posterior edge of insertion to anterior edge of Eb2.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 narrowly on posterior edge of mid-posterior bony Eb4 process lateral to uncinat process.

LP broadly on Eb4 dorsoposteriorly, beginning at LE4 insertion and extending well laterally.

LI1 on Pb2 dorsoanterior process just ventral to articulation with IAC.

LI2 on Pb3 dorsolaterally just anterior to medial end of Eb3.

Remarks. Stiassny (1990:6–7; 1993:200–202) first proposed that the separation of the origin of LE1 from those of the other LEs by the origins of LI1 and LI2 is a synapomorphy of the Mugilidae and Atherinomorpha. The separation occurs in our specimens of *Agonostomus*, but it appears that it involves only LI2.

TD comprises TPb2d, TPb2, TEb2, and TPb3. TPb2d, TPb2, and TEb2 originate from mid-longitudinal raphe which gives rise dorsally to flimsy CT sheets and is attached anteroventrally to CT of pharyngeal roof. TPb2d very broad, broadest anteriorly; attaches on dorsolateral half of IAC; central portion of muscle overlaps most of central portion of TEb2; laterally, beginning at medial surface of LI1 and continuing posteriorly, TPb2d overlaps most of TPb2. TPb2 relatively thick, anterolaterally curving muscle on each side passing dorsal to TEb2 mid-laterally and attaching anteriorly to IAC posteromedially at joint with Pb2. TEb2 extends laterally onto dorsoanterior half of Eb2 well medial to LE2 insertion. TPb2d, TPb2, and TEb2 not connected posteriorly with TPb3, which is ventral to OD3–4; TPb3 on Pb3 dorsoposteriorly just medial to medial ends of Eb3 and Eb4.

Remarks. Attachment of TPb2 (including TPb2d) primarily to IAC occurs infrequently in acanthomorphs, but most extensively, and probably homoplastically, only in Mullidae, Moronidae, and Epiplatidae.

OD3–4 origin on Pb3 dorsomedially ventral to TEb2, insertion on dorsoanterior surface of Eb3 uncinat process and dorsomedial edge of Eb4 uncinat process.

OP dorsally on Eb4 posteriorly beginning a little medial to uncinat process and extending laterally to bony process supporting LE4 insertion, overlapping LE4 posteromedially; ventrally on bony flange extending posteriorly from Cb5 posterodistally, meeting Ad5 posteriorly.

Ad1 absent (small area of GFM spans Eb1–Cb1 joint anteriorly).

Ad2 begins medially at raphe with lateral end of TEb2, extends along anterior surface of Eb2 and spreads across Eb2–Cb2 joint.

Ad3 begins slightly lateral to anteromedial end of

Eb3, extends laterally along anterior surface of Eb3 and spreads across Eb3–Cb3 joint.

Ad4 on ventral surface of Eb4 beginning medially anterior to OP and extending laterally to near posterodistal end of bony edge; ventrally, attaches for equal extent along bony dorsal surface of Cb5 medial to Eb4–Cb4 joint.

Ad5 dorsally beginning on cartilaginous distal end of Eb4 posteriorly and extending moderately well medially on bony surface, and on distal cartilaginous tip of Cb4 posteriorly; ventrally on distal end of Cb5 dorsoanteriorly.

Remarks. It is relatively uncommon in acanthomorphs for Ad5 to insert on the bony surface of Eb4.

SOD absent in smaller specimen, but present, thin and moderately broad in larger specimen.

RDs proximate, insert on Pb3 posteriorly.

Remarks. Harrison and Howes (1991:114) state that RD “in the majority of mugilids” they studied, which included *A. monticola*, inserts on Pb2. They did not mention which mugilids are exceptional or where RD inserts in them. They discussed the structure and origin of RD in *Agonostomus*, but did not mention its insertion. They recognized that RD insertion on Pb2 is clearly a specialization in acanthomorphs.

Harrison and Howes (1991:126) considered *Agonostomus* to be the sister group of all other mugilids, based on several characters including, among others, the slender structure of LI2 and the fact that each RD is a single muscle, as opposed to paired in most other mugilids. The insertion of RD on Pb3 in *Agonostomus* is additional evidence of the plesiomorphic position of that genus within the Mugilidae.

Additional remarks. SCL free from Bb3 (posterior cartilaginous tip small, not extended posteroventrally). TV4 free from Cb5s. Pb4 absent, UP4 present. Pb2 toothed. Eb4 levator process absent.

Both Rosen and Parenti (1981:fig. 3, AMNH 11613) and Parenti (1993:fig. 5, USNM 73742) indicated that Pb4 is present in *Agonostomus monticola*. Of these, the AMNH specimen is missing (B.A. Brown, e-mail, 02/06/2003), but we have seen Parenti’s specimens, which are small, but in our opinion lack Pb4, as do our two specimens. The absence of Pb4, a specialization, albeit moderately common among acanthomorphs, is also true of atherinomorphs and might offer support for a relationship between that group and mugilids (Stiassny, 1993); however, Harrison and Howes (1991) reported the presence of Pb4 in juvenile *Mugil cephalus*, three species of *Liza*, and *Chelon labrosus*, but made no mention of its state in *Agonostomus*. We examined a few cleared- and stained juvenile specimens of specialized (have modified Eb1) mugilids (USNM 315896, unidentified) and *Mugil cephalus* (USNM 156159), and agree

that they have Pb4. The absence of Pb4 in *Agonostomus* is thus a specialization.

A poorly developed bony Eb4 flange is present dorsolaterally, but is easily overlooked as it only slightly overlaps the cartilaginous distal end of Eb4. It is much better developed in the larger specimen and is especially apparent when Eb4 is viewed frontally rather than dorsally.

Atherinomorpha

Atheriniformes

ATHERINIDAE

Menidia peninsulae (Goode and Bean), USNM 160465, 2 specimens, 88.0–95.6 mm.

Plate 95A, B, D

Additional material. ② = *Odontesthes regia* (Humbolt), USNM 176485, 140 mm; USNM 127863, 135 mm.

BEDOTIIDAE

③ = *Bedotia* sp., USNM 301513, 48.4 mm.

Plate 95C

Description.

LE1 on Eb1 at and just lateral to base of uncinat process. ② On uncinat process dorsal to base. ③ On cartilage tip of uncinat process laterally, extending onto adjacent bony edge of process.

LE2 on tip of expanded bony dorsal edge of Eb2, viewed laterally appears to be two longitudinally fused muscles: anterior section broader, muscoulously on process; posterior section tendinous ventrolaterally, continuing posteriorly as ligament-like lateral edge of CT roofing pharynx and attaching to anterior edge of Eb3 (only CT edge shown in Plate 95.1A). ② No apparent longitudinal separation. ③ Finely on tip of expanded bony dorsal edge of Eb2, no apparent longitudinal separation.

LE3 slender, on Eb3 uncinat process. ② Inserts by long, slender tendon on tip of uncinat process.

LE4 on tip of bony process just lateral to Eb4 uncinat process. ③ Posteroventrally joins raphe with OP dorsally and except for fine attachment anterolaterally, is free from Eb4; forms sling (sensu Stiassny and Jensen, 1987).

LP narrowly or, usually, broadly on Eb4 bony surface well lateral to LE4 insertion, variably joining raphe ventrally with Ad5 or Ad5 and OP dorsally (forms sling). ② On most of bony surface of Eb4 lateral to LE4 insertion. ③ Slightly separated laterally from LE4 insertion; on one side, a muscle filament continues dorsally with OP (here not considered a sling).

LI1 on Pb2 just medial to attachment of IAC to

Pb2. ③ On bony surface of Pb2 well medial to IAC attachment.

LI2 on Pb3 posterolaterally and ventral to OD4 and medial end of Eb3.

TD comprises TPb2a, TPb2, TPb3, and TEb4. TPb2a attaching to broad, cartilaginous anterior end of Pb2 ventrally, completely ventral to and paralleling anterior portion of TPb2; muscle fibers mesh dorsally with those of TPb2 just posterior to a horizontal anterior to the separation of the two muscles. TPb2 roughly oblong, attaching to, and covering most of, broad cartilaginous anterior end of Pb2 dorsally, with irregular median raphe obscured by, and giving rise dorsally to, muscle straps changing to CT (CT not illustrated), which attaches to skull, and ventrally joining to TPb2a and ventromedian CT. CT extends posteriorly from muscle straps and covers Pb3 articulating facets. TPb3 completely separated posteriorly from TPb2 and TPb2a, passing posteroventral to Pb3 dorsal articulating facets and attaching to Pb3 dorsoposteriorly medial to LI2 insertion and anterior to Pb3 articulation with Eb4 medial end, continuous by diagonal strand of muscle with TEb4. TEb4 on posteromedial surface of Eb4 near dorsolateral end of OP. ② ③ TPb2 and TPb2a completely fused—no horizontal separation mid-anteriorly.

OD3 absent. ③ Present, see OD4.

OD4 origin on Pb3 dorsomedially, beginning anterior to flat dorsal articulating facet and ending on surface of Pb3 just ventral to facet; insertion on dorsal surface and medial edge of Eb4 uncinat process. ③ OD3–4 present, origin as in *Menidia*, but insertion includes anterior surfaces of Eb3 and Eb4 uncinat processes.

Remarks. Eb3 and Eb4 uncinat processes are appressed and bound to each other by CT, such that in *Menidia* and *Odontesthes* it appears that the anterior edge of OD4 insertion includes the medialmost edge of the Eb3 uncinat process. However, slicing through the separation of the two processes indicates that all of the insertion is on Eb4.

OP dorsally broadly on posterior surface of Eb4, ventrally on posterodistal bony process of Cb5. ③ OP ventrally broadly joining raphe with OP, which is mostly released from Eb4.

Ad1–3 present, each attaches along most of anterodistal edge and surface of respective Eb and to anterodistalmost tip of respective Cb. ③ Ad1 absent.

Ad4 dorsally on ventrolateral edge of Eb4, there meeting OD4 ventrally; ventrally on Cb4 dorsally immediately medial to Eb4–Cb4 joint; completely obscured from posterior view by Ad5 and OP.

Ad5 dorsally on posterodistal surface of Eb4, ventrally attaching to distal edge and dorsal surface of Cb5 posterodistal bony process.

SOD absent.

RDs proximate.

Additional remarks. SCL attached mid-dorsally to posteroventral cartilaginous tip of Bb3. TV4 free from Cb5s, which are not ankylosed. Pb1 and Pb4 absent, UP4 present. Pb2 toothed. Eb4 levator process absent.

Cyprinodontiformes

APLOCHEILIDAE

Rivulus marmoratus Poey, USNM 293487, 62.7 mm.

Plate 96

Description.

LE1 on Eb1 dorsodistally (no uncinat process).

LE2 on Eb2 dorsodistally.

LE3 on Eb3 slightly lateral to uncinat process, insertion continues posteriorly on ligament joining Eb3 and Eb4.

LE4 massive, on dorsolateral half of Eb4.

LP narrowly on Eb4 at and posterior to lateral end of LE4 insertion.

LI1 on Pb2 dorsoanterolateralmost surface just medial to IAC attachment.

LI2 on Pb3 posterolaterally anterior to medial end of Eb3.

TD comprises TPb2a, TPb2, TPb3, and TPb3p. TPb2a on ventroanterior surface of Pb2 and along medial margin of LI1 insertion, continuous with Pb2 along mid-longitudinal raphe, which gives rise to CT pad attaching to skull. Ventral surface of raphe attaches to CT sheet covering Pb3 articulating facets. TPb2 anteromedially joins longitudinal raphe and medially joins CT sheet covering articulating facets; laterally, TPb2 attaches to Pb2 dorsoanteromedial surface, dorsomedial to LI1 insertion; ventromedially, TPb2 joins CT junction with OD4 dorsoanteriorly, and posteromedially joins CT junction with TPb3 anteriorly (CT junction attaches to Pb3). Median longitudinal raphe weakly represented on semicircular TPb3, which is weakly attached mid-ventrally to CT between Pb3s, but is unconnected to TPb3p. Anteroventrally, muscle fibers of TPb3 mesh with those of OD4. TPb3p finely, tendinously attached to posterior edge of Pb3 slightly medial to joint with Eb4; SO fibers join tendinous attachment.

OD3 absent.

OD4 originates anteriorly ventral to TPb2 on dorsoanterolateral surface of Pb3 dorsal articulating facet (joining CT there with TPb2), and posteriorly ventral to TPb3 on CT covering facet, there joining with TPb3 anteriorly; inserts on broad mid-dorsal shelf on Eb4.

OP dorsally very broadly on Eb4 posterior surface, ventrally on posterodistal flange of Cb5, laterally essentially continuous with Ad5.

Ad1–3 very broadly on respective Eb, spanning

respective joint with Cb anteriorly and continuing with CT supporting strip with gill rakers.

Ad4 very broadly on ventrolateral surface of Eb4, and equally so on dorsal surface of Cb4, completely obscured from view posteriorly by OP and Ad5 (only visible in lateral view if obscuring CT and gill rakers are removed).

Ad5 medially inseparable from OP, anterolaterally attaching to distal ends of Eb4 and Cb4, ventroposteriorly to distal end of Cb5.

SOD absent.

RDs proximate.

Additional remarks. SCL band-like (as opposed to more typical threadlike in other fishes), attached mid-dorsally to cartilaginous ventroposterior tip of Bb3. TV4 attached dorsally to Cb5s (continuous ventrally). Pb1 and Pb4 absent, UP4 present. Eb3 and Eb4 uncinat processes present. Eb4 levator process absent.

CYPRINODONTIDAE

Cyprinodon variegatus Lacepède, USNM 107023, 3 specimens, 48.1–49.0 mm.

Plate 97

Description.

Remarks. Assignments of LE1 and LE1', LE2 and LE2', and LE4 and LE4' are arbitrary designations.

LE1 on Eb1 just lateral to articulation with IAC, joins raphe with Ad1 along anterior margin of insertion.

LE1' on Eb1 slightly lateral to LE1 insertion.

LE2 on posterodistal end of Eb2.

LE2' laterally appressed to LE2 on posterodistal end of Eb2. Fine ligament extends from posterior edge of LE2 and LE2' to distal end of Eb3.

LE3 absent; possibly represented by LE4'; see discussion in Additional remarks section.

LE4 on Eb4 dorsally lateral to dorsalmost point.

Remarks. LE4 and LE4' appear to be one massive muscle before mechanical separation, but separation point was same in all three specimens.

LE4' on Eb4 at and lateral to LE4 insertion; very fine ligament connects tip of Eb3 uncinat process with LE4' insertion; see discussion in Additional remarks section.

LP on dorsodistalmost end of Eb4.

LI1 on cartilaginous dorsoanteriormost tip of Pb3; in one specimen a few muscle filaments attach to dorsoanteriormost tip of Pb2 on one side and to IAC on the other.

LI2 on Pb3 dorsolaterally.

TD comprises TPb2a, TPb2, and TPb3-Eb4. TPb2a on anterior surface of dorsoanteriormost Pb2 process, joined to TPb2 along mid-longitudinal raphe, which gives rise dorsally to CT pad covering muscles. TPb2 on posterolateral surface of Pb2 dor-

soanteriormost process; TPb2 and TPb2a completely, although only narrowly separate from each other on lateral surface of process. TPb3-Eb4 attachment, tendinous, very fine, unclear, appearing variably to attach at Pb3-Eb4 joint, only to Pb3, or only to Eb4.

OD3 absent.

OD4 originates on medial surface of Pb3 beginning musculously anteriorly on lateral surface of dorsoanterior process becoming CT posteriorly and attaching to groove ventral to articulating process; insertion splits distally with anterior branch on Eb4 uncinuate process and posterior branch on Eb4 dorsal surface medial to LE4 insertion.

OP dorsally broadly on Eb4 posterior surface, ventrally on dorsodistal surface of Cb5; CT medial to OP covers Eb4-Pb3 joint.

Ad1 with two continuous portions, dorsally on medial end of Eb1 at anterior edge of LE1 insertion ventrolaterally, passing over Eb1-Cb1 joint and attaching to dorsoanterior surface of Cb1, continuous dorsally with ventral surface of crossing portion, which attaches on Eb1 medially and to gill-raker and gill-filament strip laterally.

Ad2 with two continuous portions, ventral portion attaching along most of dorsal surface of Eb2 passing over Eb2-Cb2 joint and attaching to Cb2; dorsal crossing portion beginning at medialmost end of Eb2 and extending laterally and attaching to gill-raker and gill-filament strip.

Ad3 with two continuous portions, ventral portion on Eb3 anteromedial surface and Eb4 ventroanterior surface, extending ventrolaterally and attaching to dorsoanterior surface of Cb3; dorsal portion attaching to most of medial arm of Eb3, extending laterally and overlapping and joining dorsal surface of ventral portion and attaching to gill-raker and gill-filament strip.

Ad4 dorsally on ventral surface, ventrally on dorsal surface of Cb4 medial to Eb4-Cb4 joint; obscured in posterior view.

Ad5 on posterodistal end of Cb4 and anterior surface of Cb5 well medial to distal end.

Additional remarks. SCL attached mid-dorsally to ventral surface of cartilaginous posterior end of Bb3. TV4 absent. Pb1, Pb4, and UP4 absent (or UP4 fused to Pb3, according to Parenti 1981:417, but treated by us as absent. Unless it can be shown, perhaps ontogenetically, that UP4 fuses to Pb3 in some cyprinodontids, it is equally parsimonious to treat UP4 as absent as it is to treat it as fused to Pb3). Pb2 toothed. Eb4 levator process absent.

Beloniformes

ADRIANICHTHYIDAE

Xenopoecilus oophorus Kottelat, USNM 340431, 2 specimens, 57.4–69.3 mm.

Plate 98

Additional material. ② = *Oryzias latipes* (Temminck and Schlegel), 2 specimens, 29.0–29.4 mm.

Description.

LE1 on dorsal end of IAC, which is attached mainly to dorsolateral end of Eb1 and less so to dorsolateral end of Cb1 (see also remarks following LCb2). ② IAC absent, LE1 attached to lateral end of Eb1 dorsally.

Remarks. IAC typically joins Eb1 and Pb2 in acanthomorphs. This is also true of IAC in atheriniforms such as *Cyprinodon* (Plate 97), which, similar to adrianichthyids, has lost the Eb1 uncinuate process. It seems a relatively short transition to change, for example, from the cyprinodontid state to that of the adrianichthyids (compare Rosen and Parenti, 1981: figs. 10 and 11, who recognized the states of IAC in both groups).

LE2 on Eb1 dorsodistally medial to LE2', vertically or slightly anteriorly directed toward origin.

LE2' on Eb1 dorsodistally lateral to LE2, dorso-posteriorly directed toward origin.

LCb2 on dorsal end of dorsally autogenous cartilaginous end of Cb2. ② On dorsal end of Cb2.

Remarks. The cartilaginous dorsoanteriormost ends of Cb2, Cb3, and Cb4 are greatly expanded in adrianichthyids and vary from continuous to autogenous, and that of Cb4 may consist of several separate pieces of cartilage. It is also possible that AC1 (see LE1 above) represents an autogenous piece of Cb1, but its position relative to the Eb1-Cb1 joint differs from those of Cb2–4.

LE3 absent (see remarks following LCb5).

LE4 on bony dorsoposterior surface of Eb4.

LP on dorsodistal end of Eb4 and autogenous cartilaginous end of Cb4 (not visible in Plate 98), fusing ventromedially with LCb5 laterally and with Ad5 ventrolaterally. ② On Eb4 mid-dorsally and cartilaginous distal end of Cb3 dorsally. See remarks following LCb2.

LCb5, as it extends toward Cb5, attaches anterolaterally to posterolateral surface of distal end of Eb3 (attachment released in Plate 98A, C), joins anteroventromedialmost surface of LP on Eb4 and posterodistalmost surface of Cb4 just lateral to ventral attachment of Ad4, and has major portion of insertion on Cb5 dorsoanterodistalmost surface anterior to Ad5 (origin was not recorded).

Remarks. Aside from these two genera, we observed LCb5 otherwise only in the ostariophysan cyprinids, in which the muscle inserts exclusively on Cb5. The homology of LCb5 is problematic, and the muscle possibly represents a highly modified LE3.

LI1 on dorsoanterior tip of Pb2 posteriorly.

LI2 broadly on Pb3 dorsoposterolaterally.

TD comprises TPb2, TPb2a and TPb3. TPb2 has median longitudinal raphe and attaches to Pb2 dor-

soanterior process dorsal to TPb2a. TPb2a attaches to anteroventral edges of Pb2 dorsoanterior process and is continuous posterodorsally with TPb2. TPb3 attaches to Pb3 in groove ventral to Pb3 articular surface with Eb4.

OD3 absent.

OD4 originates on Pb3 dorsoanteromedial surface ventral to TPb2 and inserts on bony Eb4 dorsal surface.

OP dorsally on Eb4 posteroventral surface lateral to medial end and medial to Ad5 dorsomedially, ventrally on Cb5 dorsodistally, only weakly separated from Ad5 laterally.

M. Eb1-IAC very fine, on Eb1 dorsolaterally and lateral surface of IAC ventral to LE1 insertion.

Ad1 absent, but long GFM present as in second arch.

Ad2 broadly on Eb2 anterior surface and CT between Eb2 and autogenous Cb2, and narrowly on, Cb2 dorsoanteriorly lateral to GFM dorsally.

Ad3 very broadly on Eb3 anterior surface and CT between Eb2 and autogenous Cb3, and narrowly on Cb3 dorsoanteriorly lateral to GFM.

Ad4 dorsally on Eb4 ventral to OD4 insertion, ventrally on Cb4 dorsodistally; muscle broad dorsally, very narrow ventrally.

Ad5 dorsoposteriorly on Cb4 distally and Eb4 beginning lateral to OP and extending to distalmost end, there joining fine raphe with ventrolateralmost edge of LP, ventrally on Cb5 distally. ② Unclear if Ad5 joins LP.

SOD absent.

RDs well separated.

Additional remarks. SCL attached dorsomedianly to cartilaginous ventroposterior end of Bb3. TV4 free from Cb5s. A strap of SO extends anteriorly just lateral to RD and inserts in a deep bony pocket in Pb3 ventrolateral to LI2. Pb1, Pb4, UP4, and Eb4 levator process absent. Pb2 toothed.

BELONIDAE

Tylosurus crocodilus (Peron and Lesueur), USNM 128454, ca. 345 mm; USNM 137545, not measured, USNM 294990, ca. 170 mm.

Plate 99

Additional material. ② *Strongylura timucu* (Walbaum), USNM 203575, ca. 225 mm.

Description.

LE1 on dorsal edge of bony process projecting medially from enlarged lateral end of Eb1.

Remarks. Based on the configuration of the lateral end of the closely related scomberesocid, *Cololabis* (Plate 100), which has a cartilage-tipped uncinat process, we consider that the uncinat process of be-

lonids has lost the cartilage tip, hence, would not be recognized as an uncinat process.

LE2 dorsally bifurcate, on posteriorly extending bony process on Eb2. ② Not bifurcate dorsally.

LE3 absent (see remarks following LE4). ② On tip of all bony Eb3 uncinat process.

LE4 (left side aberrant in illustrated specimen) on Eb4 more-or-less mid-dorsally continuing muscously anteriorly and then inserting on CT attaching Eb4 to tip of all bony Eb3 uncinat process, insertion meeting LP insertion posteromedial edge. ② On Eb3 slightly lateral to bony uncinat process, continuing onto juxtaposed Eb4, meeting LP insertion ventromedially.

Remarks. LE4 in *Tylosurus* appears to have extended its insertion a short distance anteriorly to include the tip of bony Eb3 uncinat process. The typical position of LP, at and lateral to the levator on Eb4 lends support to identification of the muscle inserting on Eb3 as LE4.

LP on Eb4 dorsodistalmost bony surface at and lateral to LE4 insertion. ② Probably present, see ② in LE4.

LI1 on Pb2 dorsoposteromedially.

LI2 relatively massive, on Pb3 dorsoposterolaterally.

TD complex, TDA comprising TPb2, TPb2', TPb3, and TDP comprising TEb4. TPb2 (see remarks following this description) attaches to anterior end of Pb2 dorsoanterior process, wraps around process, and forms raphe with itself along mid-anteroventral surface of process; anteriorly, TPb2 extends ventromedially and joins a narrow raphe-like area of CT that expands posteriorly into a broad sheet that attaches to ventral surface of skull; dorsoposteriorly, TPb2 forms a flat, shallow, thin layer (barely separate from remainder of muscle), edged medially by CT, which is continuous with broad CT sheet attaching to skull; TPb2 covers most of TPb2' and TPb3 (including dorsoanterior process of Pb3), and all three muscles join along median CT raphe-like area. TPb2' a thin, broad band passing dorsal to TPb3 and conforming with it; laterally, TPb2' attaches to Pb2 posterolaterally. TPb3 attaches to most of surface of Pb3 anteriorly, forming raphe posteriorly with OD4 on left side, and partial raphe on right side. TEb4 disconnected from remainder of SO, on Eb4 posteromedially, posteriorly continuous with SOD. Pb3's dorsoposteriorly are completely ventral to muscle, no articulating facets are exposed.

② TPb2' almost completely fused with TPb2 (TPb2' would not be recognized as such, lacking comparison with *Tylosurus*); TPb3 posteriorly attaches by CT to dorsally exposed Pb3 articulating facets, with CT continuing around facets laterally and becoming muscous OD3–4 anteriorly. TDP comprises TPb3-Eb3-Eb4 attaches to Pb3 a little medial

to medial end of LI2 continues posteriorly attaching to medial end of Eb3 and broadly along medial arm of Eb4.

Remarks. TPb2 in both species is possibly a fusion of TPb2 and TPb2a, which are separate in other atherinomorphs.

M. Pb2-Eb2 on Pb2 dorsolaterally beginning just posterior to dorsoanterior process and on Eb2 anteromedially, laterally attaching to CT between Eb1 and Eb2. ② Muscle forks immediately anterior to its attachment to medial end of Eb2; arms of fork pass to either side of LI1 and attach to separate areas, lateral and medial, on Pb2.

OD3 absent. ② OD-3-4 origin by CT on Pb3 dorsal articulating facet, insertion on Eb3 just medial to all bony uncinatate process (very fine cartilage tip) and broadly on Eb4 dorsally medial to LE4-LP.

OD4 origin dorsoanteriorly joining raphe with TPb3 posteriorly, area below raphe attaching broadly along Pb3 medially; muscle in two incompletely separated parts, lateral part passes medial to bony Eb3 uncinatate process and inserts on Eb4 dorsally medial to LE4-LP insertions, medial part inserts on Eb4 well medial to lateral part. Eb4 levator and uncinatate processes absent (both taxa).

Remarks. See similarity of insertions to those of *Cyprinodon* (Plate 97).

OP dorsally on Eb4 posterolaterally, ventrally on Cb5 posterolaterally, fusing dorsoanteriorly with Ad4 posteroventrally.

Ad1 absent.

Ad2 dorsally with anterior branch (GFM2?) attaching to dorsodistal end of Eb1 and broader attachment to anterodistal end of Eb2, and ventrally attaching to Cb2 dorsally.

Ad3 like Ad2 but anterior branch (GFM3?) on Eb2, remainder on Eb3 and Cb3; posterior branch extends medially almost to medial end of Eb3.

Ad4 attaches to Eb4 ventrally anterior to OP, posteroventrally joins anterior surface of OP and attaches to Cb4 dorsoanteriorly.

Ad5 apparently absent.

SOD present.

RDs well separated.

Additional remarks. SCL attached mid-dorsally by long tendon to posteroventral cartilaginous tip of Bb3. TV4 free from Cb5s. ② Dorsally attached narrowly to Cb5 anteriorly; ventrally free. Pb1, Pb4, and UP4 absent. Pb2 toothed. IAC absent.

AC1 present between Eb1 and Cb1 on both sides of USNM 128454 and 294990, and latter has small, questionable AC4 on both sides associated with distal end of Eb4, which is well dorsal to distal end of Cb4 (see Additional remarks in *Cololabis* on why this AC is not considered to be AC4); USNM 137545 lacks ACs on all arches. *Strongylura timucu* has AC1 on both sides, a tiny AC3 on one side, and a question-

able AC associated with Eb4 on one side. It also has, on both sides, a small disjunct cartilage associated with the distal (or dorsolateral) end of Cb2 and another with the distal end of Cb3. These two cartilages appear to be fragments of the cartilaginous distal ends of Cb2 and Cb3. The cartilages lie adjacent to the anterior bony distal ends of these two elements, each of which bears a cartilage tip posteriorly (AC3 is positioned between the cartilaginous ends of Eb3 and Cb3).

Bony flange on Eb4 distally, only slightly or not at all extending over cartilaginous distal end of Eb4, hidden by LE4-LP insertions.

SCOMBERESOCIDAE

Cololabis saira (Brevoort), USNM 320999, 3 specimens, ca. 174–220 mm.

Plate 100

Description.

LE1 beginning on cartilaginous tip of Eb1 uncinatate process and extending about half way along medially extending tendon attaching to medial end of Eb1 (free from most of anterior arm of Eb1).

LE2 on dorsally raised bony process on Eb2; lateral fibers continuous ventrally with anterior branch of Ad3.

LE3 absent (see LE4).

LE4 tendinously on Eb4 dorsally medial to distal end, tendinous insertion passes dorsoanteriorly and is applied closely on cartilaginous tip of Eb3 uncinatate process.

LP on Eb4 dorsodistally, posterolateralmost fibers ventrally variably continuous or not with OP dorsally.

Remarks. Although not as clearly forming an LP-OP sling (Stiassny and Jensen, 1987) as occurs in exocoetoids, the condition is, nevertheless a sling, which Stiassny and Jensen (1987:284) state is not present in scomberesocids; however, for this remark, they reference their fig. 2D, which is a belonid, which fishes, as opposed to scomberesocids, do not have a sling.

LI1 on Pb2 dorsally near base of anterodorsally extending Pb2 process.

LI2 on Pb3 dorsoposteriorly.

TD comprises TPb2a, TPb2, TPb3a, and TPb3p. TPb2a attaches along anterolateral edge of the long dorsoanterior Pb2 process and wraps anteriorly around process, becoming continuous with TPb2 ventromedially where they join CT of pharyngeal roof. Anterolaterally, TPb2 attaches to dorsal and medial surfaces of long dorsoanterior process of Pb2 and posterolaterally to dorsoposterior surface of Pb2, just extending onto anteromedialmost end of Eb2; along its long ventromedial length, TPb2 joins CT of midline between two sides of gill arches, to which con-

tralateral TPb2 also joins, and together join a sheet of CT lying dorsal to the flat, bony dorsoposterior facet on each Pb3; anteromedial extent of TPb2 completely overlies TPb3a. Laterally, TPb3a attaches to much of dorsal surface of Pb3, including long dorsoanterior Pb3 process, and medially attaches (together with TPb2) to CT of mid-line between two sides of gill arches; posteriorly, TPb3a continues as CT that attaches to and covers bony dorsoposterior Pb3 facet on each side. TPb3p short, joins Pb3s dorsoposteriorly, forming raphe there with SO, continuous posteriorly with SOD.

M. Pb2-Eb2 anteriorly on ventroanterolateral surface of Pb2 dorsoanterior process, posteriorly on medial end of Eb2.

OD3 absent.

OD4 originating tendinously from CT covering and attaching to dorsal surface of Pb3 medial to dorsoposterior facets, passing dorsal to flat, bony facets and most of surfaces of Eb3 and Eb4 and attaching separately to Eb4 dorsoposteriorly medial to LP and anteriorly near medial end. Eb4 uncinat process absent.

OP dorsally on most of lateral half of Eb4 posteriorly, overlapping Ad4 and Ad5 posteriorly and excluding them completely in posterior view; postero-dorsal fibers variably continuous or not with LP posteroventrally; ventrally on dorsodistal end of Cb5. A splay of fibers attaches to the posterolateral surface of Cb5, passes anterior to OP ventrally and appears to join OP dorsoanteriorly in some specimens and/or Ad5 posteromedially in others. Based on the attachment of OP to Cb5 in belonids, these fibers appear to be OP.

Ad1 absent.

Ad2 with dorsoanterior branch (= GFM2?) attaching to lateral edge of Eb1 uncinat process, continuing posteriorly, spanning area between first and second arches and attaching (Ad2) to ventral surface of Eb2 and dorsolateral surface of Cb2 anterior to Eb2-Cb2 joint.

Ad3 like Ad2 but on Eb3 and Cb3, and anterior branch (= GFM3?) attaching to raised bony process on Eb2 to which LE2 inserts.

Ad4 dorsally on dorsoposterodistalmost surface of Eb4 ventral to OP, extending medially on Eb4 anterior to OP, laterally joining distal ends and surfaces of Eb4 and Cb4 and fusing with dorsal end of Ad5 on Cb4.

Ad5 dorsally on Cb4 posterodistally, fusing there with Ad4, extending ventrally and expanding as it attaches to posterodistal surface of Cb5.

SOD present.

RDs well separated.

Additional remarks. SCL poorly defined; muscles crowded in region and attached to CT, which is attached mid-dorsally to very elongate posteroventral

cartilaginous tip of Bb3. TV4 ventrally free from Cb5s, but dorsally attaching narrowly, weakly to anterior end of Cb5 (Cb5 a single bone). Pb1, Pb4, and UP4 absent. IAC absent. Two specimens have tiny AC1 bi-laterally, and one of these has very fine, somewhat rod-shaped cartilage between lateral ends of Eb4 and Cb4 on both sides; the third specimen lacks ACs and the cartilage between Eb4 and Cb4. It is doubtful that the cartilage between Eb4 and Cb4 in *Cololabis* and belonids is homologous with AC4 of other fishes. The cartilage in the former two groups is close to the distal end of Eb4 and well separated from the distal end of Cb4. In belonids, the cartilage appears to have budded off Eb4, whereas, as far as is known, AC4 buds off the distal end of Cb4 in non-atherinomorphs.

Cololabis is the only atherinomorph we examined that appears to lack an Eb4 flange.

HEMIRAMPHIDAE

Hemiramphus far (Forsskål), USNM 294231, 2 specimens, 105–111 mm.

Plate 101

EXOCOETIDAE

Additional material. ② = *Exocoetus obtusirostris* Günther, USNM 198465, 92.8 mm; USNM 295036, 161 mm; USNM 298987, 98.8 mm.

Description.

Remarks. The muscles of *Exocoetus* appear to be more specialized than those of *Hemiramphus*, although comparing muscles of the latter with those of the former, made it possible to identify most of them. We abbreviated descriptions of Ads, LEs, and sling of *Exocoetus*.

LE1 tendinously on bony and cartilaginous tip of Eb1 uncinat process. ② Tendinously and muscoulously on dorsalmost tip of expanded lateral end of Eb1, continuous posteroventrally with CT joining Eb1 and Eb2 dorsodistally; uncinat process absent.

LE2 fan-like or split dorsally, incompletely divisible into anterior and posterior sections, which fuse at insertion on bony process near distal end of Eb2. ② Similar but inserts on dorsodistal bony edge of Eb2.

Remarks. Small, cartilaginously tipped uncinat process on Eb2 medial to bony process in both specimens (absent in *Exocoetus*). Among ctenosquamates, examined, a cartilage tipped Eb2 uncinat process is otherwise present only in some specimens of *Pholidichthys* (Pholidichthyidae).

LE3 slender, inserts by long, slender tendon confluent with fine ligament joining Eb3 uncinat process with bony dorsolateral edge of Eb4 directly posterior (medial to Eb4 uncinat process); confluence

is usually on bony edge of Eb4 but may be on ligament mid-way between Eb3 and Eb4; muscular portion united with anterior surface of LE4, but easily and discretely separated. ② Muscular portion of LE3 less easily separated from LE4.

LE4 massive, mostly free from Eb4, but narrowly attached medially to posterior surface of Eb4 uncinate process at dorsolateral edge of OP; continues ventrally becoming tendinous, with OP joining tendon dorsoanteriorly and Ad5 posteromedial surface joining tendon laterally, and together continuing tendinously and inserting on Cb5 dorsodistally (Ad5 attachment continues muscously on dorsomedial edge of Cb5); muscle variously, broadly forked ventral to origin.

Remarks. Stiassny and Jensen (1987) first noted the LE4-OP sling of exocoetoids and its similarity to that of their labroids; however, the exocoetoid LP does not participate in the sling in the same way it does in some labroids.

LP on dorsolateral surface of Eb4 and dorsoposterior edge of Cb4, relatively distinct and separate from LE4. ② Muscle joins LE4 insertion laterally and wraps closely around LE4 posteromedially.

LI1 on ventrolateral surface of elevated Pb2 anterior process.

LI2 on Pb3 dorsolaterally, posterior portion of insertion passing ventral to OD4 anteriorly. ② On Pb3 posterolaterally.

TD complex, comprising TPb2, TPb2a, TPb2v, TPb3, and TEb4. TPb2 comprises separate muscle on each side, inserting broadly along ventral surface of cranium (muscle is considerably truncated in Plate 101); each side has broad fascia attachment on dorsal Pb2 process dorsoanteriorly and muscle generally covers TPb3, obscuring it dorsally. TPb2a completely separate from TPb2, attaches to medial edges of dorsal Pb2 processes; muscle may represent a separation from TPb2, which wraps around Pb2 in various atherinomorphs (see *Tylosurus*, Plate 99). TPb2v superficially appears to be bilaterally paired muscle, but fibers fuse across ventral midline; anteriorly muscle attaches to skull, posteriorly attaches to ventroanterior edge of Pb2. TPb3 joins ventroanterior surfaces of Pb3 anterior processes (Pb3s are fused, but deeply cleft, ventromedially), has median longitudinal raphe. TEb4 arising on each side from lateral edge of CT sheet, passing dorsal to posterior surfaces of Pb3 apophyses, and joining opposite TEb4; muscle inserts on Eb4 uncinate process immediately posterior and essentially continuous anteriorly with OD4. SO muscle strap from each side joins edge of CT sheet posterior to TEb4 posterior edge.

② Composition same, muscles differently disposed; TPb3 and TEb4 are unpaired. TPb2 much less extensive, attaches dorsolaterally on Pb2 dorsoanterior process, extends membranously around Pb2 and

Pb3 anterior processes encapsulating fatty and/or glandular mass of tissue; thins and fans out posteriorly and overlaps TPb3, extends ventromedially and very weakly attaches along midline between Pb3s and possibly dorsoposteriorly to cranium. TPb2a well developed, triangular, apex attaching to dorsomedial surface of Pb2 dorsoanterior processes, extends ventromedially toward midline and attaches to skull. TPb2v originates on ventrolateral surface of Pb2 dorsoanterior process and extends anterolaterally to anteromedial end of Eb1, to which it is weakly attached by CT; posteromedially weakly attached to skull. TPb3 a narrow band of undivided muscle with mid-longitudinal raphe, situated in area between posterior ends of bases of Pb3 dorsoanterior processes and Pb3 posterodorsal articulating facets; lateral ends extend anteriorly as CT and attach to Pb3 dorsoanterior process. TEb4 interrupted at lateral edge of Pb3 dorso-posterior facet but continuous with CT across top of facets with opposite TEb4, muscle uninterrupted as it passes posterior to Pb3 posterodorsal articulating facets, attaches laterally to distal ends of Eb4s.

OD3 absent.

OD4 originates broadly on Pb3 dorsal surface lateral to anterolateral edge of Pb3 dorsoposterior facet and inserts on Eb4 uncinate process. ② Originates on Pb3 posterodorsally anterior to articulating facet and medial to LI2 insertion; inserts on Eb4 uncinate process.

OP narrow muscle strap on posterolateral surface of Eb4, joining LE4 ventrally (see LE4 description, also remarks following LE4), extending ventrally and inserting on Cb5. ② Similar, but free portion dorsolaterally continuous with "sling."

Ad1 absent.

Ad2 on entire ventral edge of Eb2 and dorsoanterior edge of Cb2; small IAC associated with dorsoanterior edge of muscle. ② Present, IAC similar.

Remarks. Rosen and Parenti (1981:fig. 12) show IAC in exocoetoids as extending between Eb1 and Eb2. The size of IAC in our specimens varied from a small sphere to a moderate-sized rod similar to that in Rosen and Parenti (1981:fig. 12A).

Ad3 bipartite, anterior branch on tip of Eb2 dorsal bony process and Cb3 dorsal surface where it joins ventral portion of posterior section, which is on most of Eb3 anterior surface. ② Not bipartite (anterior portion absent).

Ad4 on ventral edge of Eb4 and dorsoposterior edge of Cb4 medial to Eb4-Cb4 joint. ② Not clearly present; possibly fused in sling.

Ad5 dorsally on Cb4 posterodistally, medial surface fusing with LP sling ventral tendinous end and attaching to Cb5 dorsodistally.

SOD absent.

RDs well separated.

M. Pb3p, cone-shaped, narrowly joined to contra-

lateral M. Pb3p anteroventrally at insertion on Pb3s posteroventral to Pb3 dorsal apophyses; cones are confined dorsally, but are free from, conforming concave bony roof formed by posterior end of skull, and are restricted ventrally by RDs and viscera; dorsally each cone has thin, traversing ribbon of muscle.

Additional remarks. SCL attached mid-dorsally to cartilaginous ventroposterior tip of Bb3. TV4 interrupted medianly and attached to ventrolateral edge of Cb5 keel. Pb1, Pb4, and UP4 absent. Eb3 and Eb4 uncinat processes present. Eb4 levator process absent. Tiny AC1 present or absent, AC2 present. ② AC1 present or absent, AC2 absent.

Perciformes

ACROPOMATIDAE

Synagrops bellus (Goode and Bean), USNM 359306, 108 mm, USNM 186122, 124 mm.

Plate 102

Description.

LE1 with tendinous origin; insertion broadly on high Eb1 uncinat process, beginning near tip and extending ventroanterolaterally almost to base.

Remarks. Ligament originates on skull immediately anterior to origin of LE1 and inserts on Eb1 anterior to LE1 insertion; ventrolaterally, ligament is continuous with low CT sheet that attaches along almost entire dorsolateral edge of raised anterior margin of Eb1.

LE2 on raised posterior margin of Eb2 at about mid-length.

LE3 on tip of Eb3 uncinat process.

LE4 on tip of Eb4 levator process anteriorly.

LP slender, on Eb4 at and lateral to LE4 insertion.

LI1 tendinously on dorsoanterior Pb2 process posteriorly.

LI2 on Pb3 posterolaterally at joint with Eb3, medial edge of insertion meeting lateral edge of TPb3-Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3; covered dorsally by tough CT sheets, which attach along entire posterior surface of Pb1s, continuing medially along anteriormost edge of Pb2s to mid-line of CT of pharyngeal roof, thence continuing posteriorly on mid-line raphe joining TPb2 and TEb2 posteriorly. TPb2 flat, thin, broadly V-shaped, with, narrow, anterior mid-line notch deeply separating arms of V; muscle completely underlain by TEb2. TEb2 flat, very broad medially, narrowing considerably laterally and attaching on Eb2 dorsally anterior to LE2 insertion; muscle continuous posteriorly by fine muscle strands with TPb3-Eb3. TPb3-Eb3 anteriorly broadly on Pb3 dorsally ventral to OD3-4, posteriorly attaching along medial edge of LI2 insertion and on

posteromedial cartilaginous end of Eb3 dorsally (passes dorsal to medialmost end of Eb4 without attaching); muscle narrows posteriorly and is continuous by crossing muscle strands with SOD.

OD3-4 origin on Pb3 dorsomedially ventral to TEb2, insertion mainly on Eb3 anterior surface beginning just ventral to tip of uncinat process and extending medially; lesser insertion on anterior edge and surface of Eb4 just ventral to tip of uncinat process.

OP dorsally on Eb4 posteriorly beginning on medialmost bony surface and extending laterally to or just lateral to uncinat process, laterally overlapping Ad4 dorsomedially; ventrally on Cb5 dorsoposteriorly, beginning medially at junction of slender "horn" of Cb5 with expanded dentate portion and continuing almost to distal tip of Cb5, there joining raphe with Ad5 posteromedially.

Ad1-3 absent (GFM1 well developed; GFM2 much reduced; GFM3 absent).

Ad4 dorsally on Eb4 posteriorly, beginning medially anterior to OP and extending to posterodistal-most bony surface; ventrally on Cb4 dorsoposteriorly a short distance medial to distal end and extending laterally almost to distal end, there joining raphe with Ad5 dorsomedially.

Ad5 dorsally on Cb4 posteriorly beginning ventral to medial end of Ad4 and extending laterally almost to distal end of Cb4, there joining raphe with Ad4 ventrally; ventrally on Cb5 dorsally anterior to OP, attaching for distance paralleling attachment on Cb4, joining raphe with OP ventrolaterally.

SOD present.

RDs moderately slender, separated by distance about equal to about half diameter of one RD.

Additional remarks. SCL weakly attached mid-dorsally to elongate, posteroventrally extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC present. Tiny AC4 present; relatively well developed in larger specimen.

Sasaki (1989:fig. 2A) partially illustrated the dorsal gill-arch musculature of *Acropoma japonicum* Günther, which appears to differ from *Synagrops bellus* in that TPb2 is apparently broadly kidney-shaped rather than V-shaped.

PERCICHTHYIDAE

Macquaria colonorum (Günther) USNM 59968, 125 mm.

Plate 103

Description.

Remarks. All LEs originate tendinously.

LE1 on anterior surface of Eb1 uncinat process ventrally.

LE2 on dorsoanterior surface of Eb2 elevated bony posterior ridge.

LE3 on Eb3 uncinat process dorsoanteriorly with CT extending ventromedially from insertion joining OD3–4 posterolaterally on Eb4 uncinat process.

LE4 on bony edge of Eb4 levator process just medial to cartilage tip, ventrolateral edge joining raphe with OP.

LP at lateral edge of LE4 insertion, extending onto cartilage tip of Eb4 levator process.

LI1 on Pb2 dorsoanteriorly; anterior edge joining raphe with TPb2 on Pb2 just medial to joint with IAC.

LI2 on Pb3 dorsal surface at and lateral to TPb3–Eb3 attachment and medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3–Eb3. TPb2 overlies TEb2, beanshaped, notched mid-anteriorly, attached to anterior cartilaginous tip of Pb2 near joint with IAC, joining raphe with ventromedial edge of LI1; muscle with mid-longitudinal raphe, anterior end of which attaches to CT of pharyngeal roof and to Pb3 anterior end dorsally; raphe giving rise dorsally to CT mass covering muscle, ventrally joining TEb2, posteriorly continuing across middle of TEb2. TEb2 attaching laterally along medial half of Eb2 dorsal surface and lateral to LE2 insertion, continuous posteriorly by slender, diagonal strap of muscle with anterior end of TPb3–Eb3. TPb3–Eb3 on Pb3 medial to medial edge of LI2 insertion and dorsal surface of medial end of Eb3, continuous posteriorly by crossing muscle straps with SOD.

OD3–4 on dorsoanterior surface of Pb3, insertion on anterior surface of Eb3 uncinat process and anterior surface and medial edge of Eb4 uncinat process.

OP broadly on most of Eb4 posterior surface joining raphe with ventrolateral edge of LE4 insertion, ventrally, narrowly on posterodistal surface of Cb5, medially not clearly separable from SO; bilaterally asymmetrical, left side appearing to comprise two straps of muscle, right side only one.

Ad1–3 absent.

Ad4 dorsolaterally on Eb4 levator process posterior surface lateral to OP, and medially on Eb4 ventral surface anterior to OP, ventrally on dorsoposterior surface of Cb4 medial to Eb4–Cb4 joint and anterior to Ad5.

Ad5 on dorsal surface of Cb5 distally anterior to OP attachment and on Cb4 posterodistal surface posterior to Ad4 attachment, with dorsodistal portion of muscle continuous with tough CT (not illustrated) attaching broadly to AC.

SOD present.

RDs separate, adjacent.

Additional remarks. SCL attached mid-dorsally to posteroventral cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. AC4 present.

LEPTOBRAMIDAE

Leptobrama muelleri Steindachner, WAM P.556-001, 195 mm.

Plate 104

Description.

LE1 shortest levator; tendinously and muscously on Eb1 beginning just lateral to tip of horizontally directed uncinat process and continuing medially onto tip and on to IAC dorsolaterally. LE1 and Eb1 tightly attached anteriorly to CT lining gill chamber.

LE2 on tip of dorsally projecting peg-like process arising from Eb2 dorsoposteromedially; ventrolateral surface continuous with CT extending anteriorly around, and attaching to, LE1 and Pb1.

LE3 narrowly joining OD3–4 just anterior to tip of Eb3 uncinat process and extending to CT covering (joining) Eb3 and Eb4 uncinat processes, there joining LE4 insertion.

LE4 (see also LE3) beginning on CT enveloping Eb3 and Eb4 uncinat processes and continuing short distance posteriorly to point just medial to tip of Eb4 levator process, there joining LP ventromedially.

LP on Eb4 beginning at ventrolateral edge of LE4 insertion and extending to bony end of Eb4, there joining CT attaching to PP; tough fascia extends medially from PP, attaches to lateral edge of OP and covers OP and Ad5 posteriorly, also infiltrates SO laterally.

LI1 on Pb2 dorsoanteriorly.

LI2 on Pb3 posterolaterally adjacent to anteromedialmost edge of Eb3, muscle fibers posterolaterally just failing to meet anterolateral edge of TPb3–Eb3–Eb4 muscle fibers.

TD comprises TPb2, TEb2, and TPb3–Eb3–Eb4. TPb2 comprising a pair of semicircular muscle bands overlying the mid-section of TEb2; bands join raphes mid-anteriorly and mid-posteriorly and attach anterolaterally to Pb1, anteroventrally to dorsomedial edge of IAC and joint with Pb2, and also medial edge of LI1 dorsal to insertion; anterior and posterior junctions of muscle bands attach ventrally to CT of pharyngeal roof; muscle bands surround central tough CT area forming TEb2 mid-section, which is dorsal to dorsomedial surfaces of Pb3s. TEb2 consisting of anterodorsal broader section and posteroventral narrow section joined medially by tough CT to contralateral muscle sections; muscle extends laterally onto Eb2 to position anterior to LE2 insertion. TPb3–Eb3–Eb4 free from TPb2–TEb2 posteriorly; beginning anteriorly on Pb3 near ventromedial edge of LI2 insertion, continuing posteriorly a short distance and attaching to posteromedialmost edge of Eb3 and to dorsomedial surface of Eb4; muscle continuous posteriorly by slender, diagonal muscle strand with SOD.

OD3–4, OD3' originate together on Pb3 dorso-

medially and branch shortly after exiting from under TEb2 into OD3–4 dorsally and OD3' ventrally. OD3–4 inserts on Eb3 bony surface ventral to tip of uncinat process and on posteromedial edge of bony support of Eb4 uncinat process, joining raphe with OP dorsally beginning just medial to tip of levator process and extending medially. OD3' inserts on Eb3 dorsally ventral to uncinat process.

OP dorsally on Eb4 posteriorly beginning at about mid-length of Eb4 and extending laterally to small bony process just medial to tip of levator process, joining raphe for most of its dorsal extent with OD3–4; laterally, OP overlaps medial half of Ad4 on Eb4; lateral edge of OP tendinous, continuous as CT sheet giving rise to PP; ventrally OP on Cb5 dorsoposteriorly, ventrolaterally joining raphe with Ad5.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly, beginning well medial to lateral end of OP and extending laterally almost to distal end of bone (not including cartilage), ventrally on Cb4 dorsally, extending from near inner angle of Eb4–Cb4 joint for distance equal to dorsal attachment, meeting Ad5 dorsoanteriorly on Cb4.

Ad5 dorsally on AC4 medially and Cb4 beginning near posterodistal surface and extending medially a relatively short distance, meeting Ad4; ventromedially joining raphe with OP ventrolaterally.

SOD present.

RDs slightly separated.

Additional remarks. SCL present, attached mid-dorsally to tip of elongate, ventroanteriorly curving cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Medial end of Eb4 smaller than that of Eb3. Pb2 toothed. PCI begins at distal end of Cb5 and extends broadly medially, does join raphe with OP, but appears to join CT covering Ad5 anteriorly.

LATIDAE

Lates niloticus (Linnaeus), USNM 332869, 61.3 mm; USNM 332870, 123 mm, USNM 166851 (2): cleared and stained.

Plate 105

CENTROPOMIDAE

Additional material. ② = *Centropomus undecimalis* (Bloch), USNM 194201, 2:71.4–114 mm.

Not illustrated

Remarks. Mooi and Gill (1995:129–130) argued that the two synapomorphies Greenwood (1976) used to recognize a single family, Centropomidae, comprising two subfamilies, Centropominae and Latinae, are invalid. They, therefore, recognized the two subfamilies as families, with unresolved interrelationships. We find very little difference between the two families in their dorsal gill-arch musculature.

Description.

LE1 short, broadly on Eb1 uncinat process anteriorly just ventral to tip.

LE2 on raised posterior rim of Eb2 posterior to distal end of TEb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 dorsoposteriorly well lateral to uncinat process, joining raphe with Ad4 dorsomedially and joined posteroventrolaterally by LP.

LP on Eb4, extending medially from dorsodistal-most bony edge to, and joining, LE4 posteroventrolaterally; CT joins ventrolateral edge of LP with PP.

LI1 on dorsoanteriormost surface of Pb2 immediately medial to medial end of IAC and immediately lateral to anterolateralmost edge of Pb3.

LI2 on Pb3 dorsoposterolaterally just medial to medial end of Eb3, meeting lateral edge of TPb3.

TD comprises TPb2, TEb2, TPb3–Eb3. TPb2 flat, kidney-shaped, incurved anteriorly, divided by mid-longitudinal raphe that continues posteriorly across TEb3; raphe attaching ventroanteriorly to pharyngeal roof CT, giving rise dorsally to thin, tough CT sheets, which also attach anterolaterally to dorsoanterior surface on each side of TPb2; TPb2 attached anterolaterally to Pb2 dorsoanteriormost edge and anterior edge of LI1 slightly dorsal to insertion. TEb2 almost completely underlying TPb2, with fibers of both muscles meshing on each side of mid-longitudinal raphe. TEb2 extending laterally to medial edge of raised anterior rim of Eb2, directly anterior to LE2 insertion. TPb2 and TEb2 free from TPb3–Eb3. TPb3–Eb3 attaches to Pb3 posterolaterally, meeting medial edge of LI2 insertion and attaching tendinously to posteromedialmost corner of Eb3. TPb3–Eb3 continuous posteriorly by diagonal muscle strands with SOD.

② TD comprises TPb2, TEb2, and TPb3. TPb2 V-shaped, arms broad, otherwise similar to *Lates*.

OD3–4, 3' origin on Pb3 dorsoanterioromedial edge and surface, insertion on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process. OD3' present on one side in smaller specimen, but not present in larger specimen; separates ventrally from OD just ventral to origin and extends onto Eb3 dorsally to position ventral to insertion of OD3–4 on Eb3. ② OD3' absent.

OP comprises two sections, a thinner medial section and thicker lateral section; dorsally, medial section begins on Eb4 posteriorly near bony medial end and extends laterally to medial edge of lateral section, which is on Eb4 posteriorly beginning just medial to bony rise of uncinat process and extending laterally to just below LE4 insertion medially; lateral section joins raphe with OD3–4 insertion on Eb4 uncinat process. Ventrally, medial section is on Cb5 well medial to distal end and overlaps lateral section posteromedially; lateral section extends laterally almost to

tip of Cb5, membranously overlapping Ad5 posteroventrally. Left side of larger specimen is anomalous in that lateral section has a separate lateral branch splitting off and joining Ad5 dorsoposteriorly. ② OP lateral section meets OD3–4 but does not join raphe with it.

Ad1–3 absent. Ad4 relatively broad dorsally, beginning on Eb4 dorsoposteriorly ventral to LE4 insertion and ventrolateral to medial edge of OP thick section and continuing to Eb4–Cb4 joint; muscle attaches on Cb4 dorsally beginning at Eb4–Cb4 joint and extending medially distance about equal to extent of dorsal attachment.

Ad5 moderate, attaching dorsally on Cb4 posterodistally near AC, and ventrally on Cb5 dorsodistally anterior to OP thick section.

SOD has mid-ventral branch that separates RDs from each other.

RDs adjacent.

Additional remarks. SCL questionably free from cartilaginous posterior end of Bb3, which is not elongate, nor extends ventrally. Pb4 and UP4 present. Larger specimen has tiny AC4s and, uniquely, AC5s (latter attached to distal end of Cb5s) on both sides; smaller specimen only has AC4s. ② SCL attached mid-dorsally by short, weak ligament to ventroposteriorly extending cartilaginous tip of Bb3. TV4 free from Cb5s. ② Larger specimen has tiny AC1s on both sides, well-developed AC4s on both sides, and tiny AC3 only on left side; smaller specimen only has AC4s, that of left side represented by two small cartilages.

CENTRARCHIDAE

Micropterus dolomieu Lacepède, USNM 332932, 2 specimens, 71.0–78.4 mm; USNM 332991, 78.9 mm.

Plate 106

Description.

LE1 on Eb1 anterolateral to tip of uncinat process.

LE2 on expanded dorsoposterior edge of Eb2 midlaterally.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 just medial to minute tip of levator process.

LP on Eb4 at and just anteromedial to ventrolateral edge of LE4 insertion.

Ll1 on dorsoanteriormost Pb2 surface, joins CT binding Pb2 and Pb3.

Ll2 on Pb3 dorsolaterally just anteromedial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3–Pb4–Eb3. TPb2 roughly heart-shaped with mid-anterior notch continuous with raphe, which widens as CT and continues across TEb2; attaching anterolaterally to dor-

solateral surface of broad cartilaginous anterior end of Pb2 and tiny AC lying dorsal to anterior end of Pb2 (see also Additional remarks); attaching midventrally to CT of pharyngeal roof; meshing posteriorly with TEb2 anteriorly. TEb2 mostly posterior to TPb2, extending laterally and attaching to Eb2 dorsally anterior to LE2 insertion; not continuous posteriorly with TPb3–Pb4–Eb3. TPb3–Pb4–Eb3 anteriorly ventral to TEb2. Attaching to Pb3 dorsally along medial edge of Ll2 insertion, continuing posteriorly and attaching to posteromedialmost edge of Eb3 and dorsomedial surface of Pb4, continuous posteriorly by fine, diagonal muscle strand with SOD.

OD3–4 origin broadly on Pb3 dorsomedially, only slightly, anteriorly ventral to TEb2; insertion massively on Eb3 uncinat process anteriorly and on Eb4 dorsal edge beginning at uncinat process and extending medially, with ventral fibers attaching separately to ventromedial edge of Eb4.

OP dorsally broadly on Eb4 posteriorly, beginning below medial edge of LE4 and extending medially; ventrally broadly on Cb5 dorsoposteriorly; medially difficult to separate from SO.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly beginning below levator process and extending medially; ventrally on Cb4 medial to Eb4–Cb4 joint.

Ad5 dorsally narrowly on Cb4 posterodistally, ventrally on Cb5 dorsally posterior to Eb4 and anterior to OP.

SOD present.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to tip of posteroventrally curving cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Tiny AC on dorsoanteriormost tip of Pb2, not found in any other actinopterygians examined. In USNM 348876, two cleared and counterstained specimens 25.6–29.4 mm SL showed no evidence of the AC, but a third specimen, 36.8 mm SL, in the same lot, had the AC autogenous on one side and as a bud on the other. A fourth cleared and counterstained specimen, USNM 348877 67.6 mm, had the AC autogenous on both sides.

Enneacanthus gloriosus (Holbrook), USNM 243828, 72.8 mm; USNM 90449, 57.4 mm.

Plate 107

Description.

LE1 on Eb1 anterolateral to tip of uncinat process.

LE2 on expanded dorsoposterior edge of Eb2 midlaterally.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 levator process anteriorly (uncinate process absent).

LP beginning on Eb4 posterior to lateral edge of LE4 insertion and continuing laterally.

LI1 on Pb2 dorsoanteriorly, joins CT binding Pb2 and Pb3, which lies ventral to Pb2.

LI2 on Pb3 dorsally just medial to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 very wide, interrupted mid-longitudinally by strip of CT, which gives rise dorsally to thick CT pad; attaches anteroventrally to Pb3 just posterior to insertion of LI1 on Pb3, mid-ventrally amidst SO fibers and CT of pharyngeal roof, and laterally on Eb2 dorsally lateral to LE2 insertion, meeting medial end of Ad2; discontinuous posteriorly with TPb3-Eb4. TPb3-Eb4 on Pb3 dorsoposterolaterally medial to medial end of Eb3, continuing posteriorly onto dorsomedial surface of Eb4; continuous posteriorly by diagonal muscle fibers with SOD.

Remarks. Of all the centrarchid taxa examined (see also additional acanthomorph material section), *E. gloriosus* is the only one lacking TPb2.

OD3–4 origin broadly on Pb3 dorsomedially ventral to TEb2, insertion massively on Eb3 uncinat process anteriorly and on Eb4 dorsal edge beginning at articulation with Eb3 uncinat process and extending medially, with ventral fibers attaching separately to ventromedial edge of Eb4.

OP dorsally on posterior surface of Eb4 medial to levator process, ventrally on Cb5 dorsolaterally, extending medially anterior to SO on Cb5, ventrolateral edge of attachment finely tendinous.

Ad1–3 moderately developed, on anterior surface of distal ends of respective Eb and Cb.

Ad4 dorsally on Eb4 posterolaterally, beginning below levator process, ventrally narrowly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally narrowly on Cb4 posterolaterally, ventrally narrowly on Cb5 dorsodistally.

SOD slender.

RDs adjacent.

Additional remarks. SCL attached mid-ventrally to ventral surface of posterior tip of Bb3. TV4 completely free from Cb5s or with a few dorsoanterior muscle strands attaching to anteriormost tips of Cb5s ventrally.

BATHYCLUPEIDAE

Bathyclupea argentea Goode and Bean, USNM 372712, 167 mm; USNM 305668, cleared and stained.

Plate 108

Description.

LE1 origin tendinous; insertion on Eb1 anteriorly just ventrolateral to tip of uncinat process. Slender

ligament originates near LE1 origin, expands broadly basally and inserts on Eb1 anteriorly beginning anterior to ventrolateral edge of LE1 insertion and extending laterally to end of Eb1.

LE2 on raised bony posterior edge at about mid-length of Eb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 beginning on tip of Eb4 levator process and extending short distance medially, joined at ventroanterolateralmost edge by LP.

LP small, short, on Eb4 at ventroanterolateralmost edge of LE4.

LI1 almost entirely on dorsoposteromedial half of surface of IAC; muscle dividing longitudinally into two sections (but appear superficially as single muscle) with separate but adjacent tendinous insertions joining CT extending medially and joining TPb2 attachment to dorsalmost surface of Pb2.

Remarks. The division of LI1 into two sections is apparently unusual. A non-homologous condition is duplicated in some gobioids, in which LI1 completely divides, with one part inserting on Pb2 and the other on Pb3. The totality of the two LI1 parts of *Bathyclupea* result in a muscle that is larger than LI2.

LI2 from origin ventrally to level of OD3–4, muscle is essentially vertical and parallels LE2 closely; on reaching level of OD3–4, muscle curves sharply anteromedially and becomes almost horizontal as it passes ventral to OD3–4 to its origin on Pb3 immediately medial to anteromedial edge of Eb3, which lies posteroventral to Eb2 medially.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 horizontally oblong, but with deep central anterior invagination; muscle completely dorsal to TEb2 and posteroventrally continuous with it; muscle attaches anterolaterally to Pb2 dorsoanteriorly at joint with medial end of IAC, there joining tendinous continuation of LI1 insertion; dorsoposterior surface of muscle with unilaterally extending slip, which continues tendinously with CT sheets covering dorsal surface of TD. TEb2 narrow longitudinally and relatively wide horizontally, exposed mid-dorsoanteriorly in gap exposed by TPb2 invagination; muscle with mid-longitudinal raphe attaching dorsoanteriorly to CT sheets covering TD and attaching anteriorly and mid-ventrally to CT of pharyngeal roof; muscle attaches on Eb2 beginning a little medial to LE2 insertion and continuing dorsolaterally to point anterior and a little lateral to LE2 insertion; continuous posteroventrally by fine, diagonal muscle strand with TPb3-Eb3. TPb3 originates on Pb3 beginning a little anterior to joint with medial end of Eb3 continues posteriorly along ventromedial edge of LI2 insertion and attaches to posteromedial surface of Eb3.

OD3–4 origin on Pb3 dorsoanteromedially; insertion on medial edge and anterior bony surface just ventral to tip of uncinat process, and on medial edge

of Eb4 beginning just ventral to tip of uncinat process.

OP dorsally on Eb4 posteriorly beginning medially about halfway to medial end of bone and extending laterally to point between uncinat process and medial end of LE4 insertion, failing to meet or overlap dorsomedial edge of Ad4; ventrally on Cb5 dorsally posterior to Ad5 ventrally, beginning a short distance medial to distal end of bone and extending laterally to distal end, above which OP and Ad5 join a raphe.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly, beginning medially ventral to levator process and extending laterally to lateral end of bone, ventrally on Cb4 dorsally beginning laterally near Eb4–Cb4 joint and extending medially about one-fourth length of bone, joining raphe with Ad5 on Cb4.

Ad5 dorsally on Cb4 dorsally beginning laterally at lateral end of bony portion and extending medially for distance parallel to that of Ad4, with which it forms raphe; ventrally on Cb5 dorsally anterior to OP, beginning laterally at lateral end of bony portion and extending medially a short distance; joining raphe with OP (q.v.)

SOD present.

RDs separated by distance equal to about half diameter of one RD.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Medial end of Eb3 larger than medial end of Eb4.

SYMPHYSANODONTIDAE

Symphysanodon berryi Anderson, USNM 370558, 128 mm; ② = USNM 204088, paratype, 85.7 mm; USNM 208500, paratype, ca. 120 mm, cleared and stained.

Additional material. ③ *S. octoactinus* Anderson, USNM 204085, ca. 80 mm; ④ *S. species*, USNM 371386, 86 mm.

Remarks. Only the main differences exhibited by ③ ④ are described.

Plate 109

Description.

Remarks. All levators and RDs are relatively slender.

LE1 origin a fine short tendon, insertion on broad Eb1 uncinat process anterolaterally just ventral to cartilage cap.

LE2 on dorsalmost tip of raised posterior edge of Eb2, posterior or just posterolateral to lateral end of TEb2; lateral fibers overlap medial fibers, such that muscle can be separated artificially into two parts with separate but juxtaposed insertions.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on bony dorsal edge of Eb4, slightly medial

to distal end, joining LP insertion medially, levator process absent. ③ ④ Inserts just medial to cartilage cap of levator process.

LP on dorsodistalmost bony edge of Eb4, joining LE4 insertion laterally. CT extending ventrally from insertion attaches to distal cartilaginous edges of Eb4, AC4, and Cb5, and is continuous with PP; no separate Eb4 levator process in any of the three specimens. ③ ④ Inserts on levator process and joins LE4 insertion.

LI1 on Pb2 dorsolaterally just ventral to cartilage cap joining IAC medially.

LI2 origin a fine tendon, insertion on Pb3 dorso-posterolaterally, just medial to medial end of Eb3; medial edge of insertion joining lateral edge of TPb3–Eb3 on Pb3.

TD flat, comprises TEb2, TPb2, and TPb3–Eb3. TPb2 and TEb2 with irregular mid-longitudinal raphe attaching dorsally to CT sheets (not illustrated), which are continuous anteriorly with CT of pharyngeal roof. TPb2 dorsal to TEb2, relatively small, broadly V-shaped, arms open anteriorly, each arm arising from mid-longitudinal raphe and extending anteriorly beyond anterior margin of TEb2 and attaching to broad, cartilaginous cap of Pb2 process that articulates with IAC medially (right-side arm deformed). TEb2 extending laterally and attaching to Eb2 dorsally at or a little medial to LE2 insertion; posterolaterally, fine, unilateral muscle strand extends diagonally posterolaterally and becomes confluent with TPb3–Eb3 dorsally. TPb3–Eb3 on Pb3 dorsally along medial margin of LI2 insertion, extends narrowly posteriorly, passing dorsal to Pb4 and attaches to Eb3 posteromedially; posteriorly, diagonal muscle strap joins SOD anteriorly. ② Mid-longitudinal raphe is straight; no muscle strands join TEb2 with TPb3–Eb3. ③ TPb2 transverse, not V-shaped; TPb3–Eb3–Eb4 present, with attachment broadly to Eb4 dorsally. ④ TPb2 apparently absent; TEb2 broad medially, attenuating anteromedially with narrow extension passing between dorsally naked Pb2 surfaces and attaching to CT of pharyngeal roof; TPb3–Eb3 present.

OD3–4 origin broadly on Pb3 dorsomedially, insertion on Eb3 uncinat process anteriorly ventral to cartilage tip and on medial edge of Eb4 uncinat process just ventral to cartilage tip. ② Insertion continues onto Eb4 uncinat process ventroanteriorly. ④ OD3' present.

OP in two sections, dorsally on Eb4 posteriorly: medial section begins medially about mid-way between medial end of Eb4 and uncinat process and extends laterally to point a little medial to uncinat process, meeting medial end of lateral section, which extends laterally to point ventral to LE4 insertion; ventrally, medial section attaches to Cb5 bony surface posteriorly beginning a little medial to distal end and extending medially for distance about equal to

its attachment on Eb4; lateral section becomes tendinous ventrally, joining Ad5 posteromedially and distal end of Cb5. ③ ④ Not divided into two sections, present as one broad section equal to the two.

Ad1–3 absent; GFM's moderately developed, parallel anterolateral edges of Ebs and Cbs.

Ad4 broadly on Eb4 dorsoposteriorly, beginning medially ventroanterior to OP lateral section and extending laterally to Eb4-Cb4 joint, ventrally on Cb4 dorsoposteriorly a short distance beginning at Eb4-Cb4 joint.

Ad5 relatively small; dorsoanteriorly on AC4 posteriorly and Cb4 posterodistally; posteriorly on distal end of Cb5 anteriorly, posteriorly joining tendinous ventral end of OP lateral section. ② Does not appear to attach to AC4. ③ AC4 absent, attaches mainly on unmodified distal end of Cb4, with tendinous continuation to contact between Cb4 and Eb4. ④ AC4 absent, but distal end of Cb4 with cartilaginous posterior extension to which Ad5 attaches.

SOD present.

RDs separated by distance equal to or greater than diameter of one RD.

Additional remarks. SCL attached mid-dorsally to long, ventroposteriorly extending cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. AC4 present in all three specimens, but absent in ③ and ④.

We examined three additional specimens: ③ = *S. octoactinus* Anderson, USNM 204085 (2), 69.8–81.4 mm SL, paratypes; ④ = *S. species*, USNM 371386, 86.0 mm SL. ③ is similar to *S. berryi* in lacking OD3', but differs in lacking AC4 or a finger-like process extending posteriorly from the cartilaginous distal end of Cb4. ③ Also differs from *berryi* in that Eb4 has a separate levator process and the distal end of the element is a cartilaginous knob, whereas in *berryi* and ④ there is no levator process and the cartilaginous distal end of the element is extended dorsally. It seems possible that the dorsal extension may be an early ontogenetic stage, and that with growth, the cartilage will ossify in its mid-portion, resulting in a separate levator process and a knob-like distal end.

EPIGONIDAE

Epigonus pandionis (Goode and Bean), USNM 159341, 95.2 mm, USNM 186123, 83.4 mm.

Not illustrated

Description.

LE1 on tip of Eb1 uncinat process anterolaterally.

LE2 on dorsalmost tip of raised bony posterior edge of Eb2 at about mid-length of Eb2.

LE3 on tip of Eb3 uncinat process.

LE4 on Eb4 dorsally just medial to tip of levator process, joining LP insertion posteriorly.

LP very slender, tendinously on Eb4 medial to tip of levator process, joining LE4 insertion anteriorly.

LI1 on Pb2 dorsolaterally just posterior to tip of dorsoanterior process, with tendinous attachment of anteroventral edge of muscle to TPb2 where TPb2 attaches on IAC medially.

LI2 on Pb3 posterolaterally, medial edge of insertion meeting lateral edge of TPb3-Eb3 on Pb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 flat, relatively narrow, beginning slightly anterior to TEb2 mid-section and extending posteriorly dorsal to anterior half of mid-section (dorsal to all of TEb2 mid-section in smaller specimen); muscle with broad, shallow notch mid-anteriorly, notch leading into mid-longitudinal raphe extending through TPb2 and most of TEb2; ventrally raphe tightly joined to CT of pharyngeal roof; anterolaterally TPb2 attaches to IAC dorsally just lateral to articulation with Pb2 dorsoanterior process, thus forming anterior half of notch with laterally extending TEb2; notch embraces medial edge of LI1, which has fine tendinous attachment to TPb2 near joint with IAC. TEb2 flat, relatively narrow, extending laterally and attaching on Eb2 dorsoanteriorly anterior or well lateral to LE2 insertion; TEb2 continuous mid-posteriorly by fine diagonal muscle strand with TPb3-Eb3. TPb3-Eb3 broadly on Pb3 dorsolaterally beginning posterior to joint with Eb2, and extending posteriorly along medial margin of LI2 insertion, abruptly and narrowly expanding posterior to insertion and attaching to Eb3 posteromedially; muscle continuous mid-posteriorly by broad crossing muscle strands with SOD.

OD3–4 origin on Pb3 dorsomedially, beginning a little posterior to anterior end; insertion variable: on left side, apparently abnormally, only on Eb3 broadly anteriorly beginning just ventral to tip of uncinat process; right side attachment on Eb3 similar, but insertion also on Eb4 beginning on medial edge just ventral to tip of uncinat process and extending a short distance anterolaterally. In smaller specimen, insertion on both sides is similar to that of right side of larger specimen (attachments to both Eb3 and Eb4).

OD3' relatively small, present only in smaller specimen; origin on Pb3 ventral to OD3–4; insertion on Eb3 dorsally ventral to, and well separated from OD3–4.

OP dorsally on Eb4 posteriorly beginning about mid-way between medial end and extending laterally a little lateral to uncinat process, ventrally on Cb5 beginning moderately medial to distal end and extending laterally beyond distal end onto Ad5 dorso-medially, there joining raphe with Ad5; muscle medially unclearly differentiated from SO laterally.

Ad1–3 absent. GFM1–3 weakly developed.

Ad4 dorsally on Eb4 posteriorly beginning medially below tip of levator process and extending lat-

erally to medial edge of cartilaginous distal end, there also attaching minimally to AC4; ventrally on Cb4 beginning medially at point ventrally opposite medial end of attachment on Eb4 (muscle ventromedially overlapped by OP) and extending laterally to medial angle of Eb4-Cb4 joint, joining raphe (not visible externally) with Ad5 anterolaterally.

Ad5 very small, dorsoanteriorly on Cb4 posteriorly a little medial to distal end, ventrally on Cb5 beginning a short distance medial to distal end and extending to distal end, dorsally joining raphe with OP ventrolaterally, and another with Ad4 ventroposteriorly.

SOD present.

RDs moderate, separated by space about half diameter of one RD (by space almost equal to one RD in smaller specimen).

Additional remarks. SCL present, but only RV4 attaches to it; appears to be fused with ventral aorta; possibly attached to elongate, ventrally curved cartilaginous posterior end of Bb3 (removing aorta would have destroyed attachment, if present). TV4 free from Cb5s. Pb4 present. UP4 present. Pb1 mostly bony.

MORONIDAE

Morone americana (Storer), USNM 61612, 99.9 mm.

Plate 110

Additional material. ② = *Morone mississippiensis* Jordan and Eigenmann, USNM 231447, >100 mm.

Description.

LE1 tendinously on anterior bony surface of Eb1 uncinat process.

LE2 on dorsoposterior surface of Eb2.

LE3 on cartilaginous tip of Eb3 uncinat process dorsoanteriorly.

LE4 on Eb4 levator process dorsodistally on one side, just proximal to dorsal tip on the other. ② Just proximal to dorsal tip on both sides.

LP origin tendinous, insertion at and ventrolateral to LE4 insertion. ② Ventroanterior to LE4 insertion.

LI1 on dorsoanteriormost bony surface of Pb2.

LI2 on Pb3 dorsoposterolaterally, at and lateral to TPb3-Pb4-Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 with mid-longitudinal raphe continuing posteriorly across TEb2, raphe attaching ventrally to CT of pharyngeal roof and dorsally giving rise to CT sheet covering TD; anteriorly, muscle attaches on most of dorsoanterior surface of IAC, posteriorly muscle is dorsal to anterior end of TEb2, to which it is fused mid-posteroventrally (no attachment to Pb2). TEb2 with dorsolaterally and ventrolaterally oriented muscle strands fusing laterally but with slightly di-

vided attachments on dorsal surface of Eb2, anterior attachment extending a little more laterally than posterior attachment, ending posteromedial to M. Pb2-Eb2 and anterior to LE2 insertion; muscle lying dorsal to, but posteriorly connected by CT and fine diagonal muscle strands with, anterior end of TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 on Pb3 dorsoposterior bony surface at and medial to LI2 insertion, on Pb4 dorsoanteriorly, and narrowly, tendinously on Eb3 posteromedialmost end, continuous posteriorly by diagonal strands of muscle with SOD. ② TPb2 on only medial third of dorsoanterior surface of IAC.

M. Pb2-Eb2 on anterolateralmost bony surface of Pb2 and dorsoanterior surface of Eb2 anterior to TEb2.

Remarks. This muscle is uncommon in acanthomorphs, but occurs at least in the ophidiids *Brotula* and *Dicrolene*, and all percopsiforms.

OD3-4 anteriorly on dorsoposterior surface of Pb3, posteriorly on anterior surface of Eb3 uncinat process and anterior surface and medial edge of Eb4 uncinat process.

OP dorsally on most of Eb4 posterior surface medial to Ad4, ventrally, narrowly on Cb5 dorsal surface, joining small, strong raphe there with ventromedial edge of Ad5; unusually well separated laterally from Ad4; a strap of SO muscle joins OP on Cb5 but does not attach to Eb4 as it continues anteriorly and joins SO longitudinal muscle fibers extending between Pb3s.

Ad1-3 absent.

Ad4 dorsally on ventral surface of Eb4 lateral to OP, ventrally on dorsoposterior surface of Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally, tendinously and muscously on posterodistal surface of Cb4 and tendinously on minute AC; ventrally on dorsodistal surface of Cb5.

SOD present.

RDs slightly separated.

Additional remarks. SCL attached mid-dorsally to cartilaginous ventroposteriorly extending tip of Bb3. TV4 free from Cb5s. Tiny AC4 and AC2 present. ② AC4 relatively well developed; AC2 absent.

SERRANIDAE

Remarks. Imamura and Yabe (2002) hypothesized a reorganization and recomposition of the Scorpaeniformes of previous authors. They recognized a scorpaenoid-serranoid sister group relationship within the Perciformes, but we have retained both groups separately within our Perciformes pending further corroboration of their findings. See also remarks following Scorpaenoidei.

Epinephelus merra Bloch, USNM 318074, 3 specimens, 68.6-92.5 mm.

Plate 111

Additional material. ② = *Anthias nicholsi*, USNM 151904, 110 mm (very similar to *E. merra*).

Description.

LE1 with tendinous origin, insertion broadly on bony anterior surface of Eb1 uncinat process.

LE2 on bony dorsoposterior edge of Eb2.

LE3 on dorsoanterior edge of tip of Eb3 uncinat process.

LE4 on dorsoposterior edge of Eb4 medial to tip of levator process.

LP slender, on Eb4 at and lateral to lateral edge of LE4 insertion. ② At and anterior to LE4 insertion.

LI1 on Pb2 dorsomedially ventral to TPb2 attachment; slightly larger than LI2. ② On dorsal surface of Pb2 dorsoanteriorly just ventral to joint with IAC.

LI2 on Pb3 dorsolaterally at anteriomedialmost end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 heart-shaped, deep notch anteriorly leading to mid-longitudinal raphe, which gives rise to dorsally to CT sheets attaching to skull; on broad Pb2 dorsoanterior process and ventroposterior end of Pb1 (Pb2 and Pb1 tightly joined by CT at this point), continuous posteroventrolaterally with TEb2. TEb2 on Eb2 anterior to LE2 insertion, continuous posteriorly by diagonal strand of muscle with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsal surface medial to LI2 insertion and anterior to Eb3 cartilaginous medial end, and on Eb3 bony surface dorsoposteromedially, continuous by diagonal strands of muscle with SOD. ② TPb2 does not attach to Pb1.

OD3-4 originates on Pb3 dorsomedially ventral to TEb2 and inserts on anterior surface of Eb3 uncinat process and anterior surface and medial edge of Eb4 uncinat process.

OP dorsally, broadly on Eb4 posteromedially beginning near levator process and extending medially; ventrally on Cb5 dorsolaterally posterior and coincident with Ad5, medially weakly separable from SO.

Ad1-3 absent.

Ad4 dorsally, broadly on Eb4 posterior surface lateral to OP; ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 on posterodistal surface of Cb4 and dorsolateral surface of Cb5 anterior and coincident with OP.

SOD with mid-longitudinal raphe, muscle fibers extend ventrally from raphe forming a short compartment on each side that isolates each RD.

RDs separate.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present.

LUTJANIDAE

Pristipomoides aquilonaris (Goode and Bean), USNM 158472, 101 mm.

Plate 112

Additional material. ② = *Hoplopagrus guentherii*, USNM 65544, 94.6 mm.

Description.

Remarks. *Hoplopagrus* gill-arch muscles are very similar to those of *Pristipomoides*; however, they are much more massive relative to the size of the specimen.

LE1 finely, tendinously on dorsal edge of Eb1 uncinat process just lateral to process tip. ② Tendinously on and lateral to tip of uncinat process.

LE2 on dorsal edge of raised posterior edge of Eb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 levator process dorsoanteriorly.

LP at and ventroanterior to LE4 insertion.

LI1 on Pb2 dorsal surface ventral to articulation with IAC.

LI2 on Pb3 dorsolaterally medial to anteromedial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 is dorsal to TEb2, with median longitudinal raphe giving rise to CT sheets attaching to skull; muscle attaches anterolaterally to CT binding dorsoanteriormost cartilaginous ends of Pb2 and Pb3 and dorsomedial surface of IAC, attaches mid-ventrally to CT of pharyngeal roof, fuses mid- and ventrolaterally with TEb2, and is posteriorly free from TPb3-Pb4-Eb3. TEb2 twisting dorsoposteriorly after passing laterally from under TEb2, attaching on Eb2 dorsoanteriorly anterior to LI2 insertion. TPb3-TPb4-Eb3 on Pb3 dorsolaterally medial to medial end of Eb3, continuing posterolaterally and passing dorsal to medial end of Eb4 and attaching to posteromedial edge of Eb3; muscle fibers delaminate from ventral surface of Eb3 portion and attach to dorsal surface of Pb4; posteriorly continuous by fine muscle strands with SOD. ② Comprises TPb2, TEb2, and TEb3. TEb3 on medial end of Eb3 dorsoposteriorly. TEb2 does not twist laterally.

OD3-4 origin broadly on Pb3 dorsomedially ventral to TEb2, insertion mostly on anterior surface of Eb3 uncinat process, weakly on anterior surface of Eb4 uncinat process.

OP dorsally on Eb4 posteriorly beginning near medial end and extending laterally almost to levator process; ventrally broadly on Cb5 dorsoposteriorly, posterior to Ad5.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteriorly beginning at levator process and extending laterally to end of bony surface; ventrally broadly on Cb4 extending laterally to Eb4-Cb4 joint.

Ad5 ventrally broadly on Cb5 dorsally beginning at distal end of Cb5, joining small raphe with OP

ventroanterolaterally; dorsally on posterodistal end of Cb4.

SOD present.

RDs separated by space about equal to diameter of one RD.

Additional remarks. SCL attached mid-posteriorly to very elongate cartilaginous ventroposterior tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present.

HAEMULIDAE

Pomadasys crocro (Cuvier), USNM 338643, 2 specimens, ca. 68–78.1 mm.

Additional material. *Haemulon scudleri* Gill, USNM 181299, 70.9 mm; *Plectorhinchus pictus* (Thunberg), USNM 192546, 83.0 mm.

Plate 113

INERMIIDAE

*② = *Inermia vittata* Poey, USNM 318643, ca. 80 mm SL.

Not illustrated

Remarks. We found no notable differences in the muscles among the three haemulid taxa. Inermiid muscles are very similar to those of haemulids, to which family they are closely related (Johnson, 1980). Additional evidence for this relationship is that the cartilage tip of the Eb1 uncinat process is attached to the medial edge of a small, raised bony flange, rather than to a distinct, rod-like arm. A somewhat similar arrangement is present in centrarchids and some sparids, e.g., *Acanthopagrus*. Aside from the fact that inermiid levators are less robust than those of haemulids, only the main differences are noted below. The inermiids and haemulids share in having the uncommon (for percomorphs) combination of absence of both SCL and SOD.

Description (based on *Pomadasys*).

LE1 origin slender, tendinous; insertion broad, on Eb1 beginning at joint of uncinat process with IAC and extending laterally to point almost half distance to distal end.

LE2 on medial edge of raised posterior margin of Eb2.

LE3 on Eb3 just anteroventral or just anterolateral to tip of uncinat process, meeting OD3–4 on Eb3. ② Inserts by long, fine tendon on tip of Eb3 uncinat process on one side, and by low, broad tendon on other.

LE4 on Eb4 levator process dorsally, just posterior to uncinat process, meeting but not joining LP medially. ② Inserts by long, fine tendon on tip of Eb4 levator process on one side, and by low, broad tendon on other.

LP broadly on Eb4 dorsally, extending medially from distal end to position just lateral to LE4 inser-

tion immediately anterior to tip of levator process, joining raphe with Ad4 dorsally.

LI1 tendinously on Pb2 dorsoanteriormost tip posteriorly, extending laterally onto adjacent IAC posteromedially (not visible in illustration) up to about one-third length of IAC; tendinous attachment to Pb2 continuous with CT joining Pb2 with anteriormost tip of Pb3 dorsally (insertion here not considered to include Pb3). ② Does not insert on IAC.

LI2 tendinously on Pb3 dorsolaterally immediately anterior to anteromedialmost edge of Eb3, well separated from TPb3-Eb3.

TD comprises TEb2 and TPb3-Pb4-Eb3. TEb2 robust, with broad, irregular central CT portion attached mid-ventroanteriorly to CT of pharyngeal roof and giving rise mid-dorsally to CT sheets attaching to skull; muscle extends laterally and attaches on Eb2 dorsally anterior to LE2 insertion, also meeting medial end of GFM2 (not illustrated) as latter extends dorsally on Eb2; muscle completely disjunct from TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 beginning on Pb3 dorsolaterally medial to mid-medial end of Eb3 and continuing onto posteromedialmost corner of Eb3 and dorsomedial edge of Pb4.

OD3–4, OD3' with joint origin on Pb3 dorsoposteromedially; relatively large OD3' splits off ventroanteriorly shortly lateral to origin and inserts on Eb3 dorsally ventrolateral to OD3–4 portion on Eb3; OD3–4 inserts massively on Eb3 uncinat process anteriorly and on Eb4 anteriorly just ventral to tip of uncinat process.

OP dorsally on Eb4 posteriorly beginning near medialmost bony end and extending laterally to medial edge of levator process, overlapping medial portion of Ad4 posteriorly; ventrally on Cb5 dorsoposteriorly beginning medially near TV5 and extending laterally almost to distal end, but becoming membranous ventrolaterally and overlapping Ad5 posteriorly; ventromedially fusing with SO.

Ad1–3 absent. GFM1–3 (not illustrated) moderately developed; GFM2 extending anteromedially, then dorsally on Eb2 to position anterior to distal end of TEb2.

Ad4 dorsally on Eb4 posteroventrally beginning anterior to OP near bony medial end and extending laterally to distalmost bony end; ventrally, moderately broadly on Cb4 laterally, becoming fused posteriorly with Ad5 anteromedially.

Ad5 dorsally on AC4 posteriorly and Cb4 posterodistally for short distance, there anteriorly joining Ad4 posteriorly; ventrally on Cb5 dorsoposterolaterally, mostly anterior to OP.

SOD absent.

RDs adjacent. ② Separated by distance equal to diameter of one RD.

Additional remarks. SCL absent; cartilaginous posterior end of Bb3 not elongate. TV4 free from Cb5s.

Pb4 and UP4 present. Pb1 with cartilaginous ends. Pb2 with teeth. AC4 present. Dorsoanterodistalmost bony margin of Eb4 and, variously, Eb2 and Eb3, with small flange in *Haemulon* and *Plectorhinchus*; flanges very reduced in *Pomadasy*, very well developed in a cleared and stained specimen (USNM 214488, 95 mm) of *Parakuhlia macropthalmus* (Osório). ② Flange clearly present, but so fine as to be easily overlooked.

APOGONIDAE

Glossamia wichmanni (Weber), USNM 344886, 2 specimens, 67.3–97.7 mm.

Plate 114 (based on smaller specimen)

Additional material. ② = *Cheilodipterus macrodon* Lacepède, USNM 276623, 82.6 mm SL.

Remarks. Differs from *G. wichmanni* mainly in having musculature much less robust.

Description.

LE1 on expanded dorsoposterior edge of Eb1 lateral to tip of uncinat process.

LE2 on expanded dorsoposterior edge of Eb2 about mid-laterally.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on expanded dorsoposterior surface of Eb4 lateral to tip of uncinat process.

LP on Eb4 at and lateral to lateral edge of LE4.

Remarks. Narrow, lateralmost cartilaginous edge of expanded dorsoposterior surface of left-side Eb4 narrowly continuous ventrally with knob-like cartilaginous distal end of Eb4. Cartilaginous lateral end continuous ventrally with knob-like distal end of Eb4 on both sides in larger specimen and ②.

LI1 on dorsoanterolateralmost surface of Pb2 just medial to articulation with IAC.

LI2 on Pb3 dorsoposterolaterally just anteromedial to medial end of Eb3.

TD comprising TPb2, TEb2, and TPb3-Eb3, with mid-longitudinal raphe extending through all components and SOD, giving rise dorsally to CT sheet covering surface of muscles, and attaching ventrally to CT of pharyngeal roof between Pb3s. TPb2 very thin, flat, bilobed, arising dorsally from mid-longitudinal raphe in common with TEb2 posteriorly; anteriorly joining raphe with TEb2 anterolaterally and at that point weakly attaching to cartilaginous anterior end of Pb2 just medial to LI1. TEb2 very broad, attaching on Eb2 dorsally anterior to LE2 insertion, continuous posteroventrally only by CT with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsoposterolaterally beginning along medial edge of LI2 insertion and continuing posteriorly, crossing over medial end of Eb4 and attaching along posteromedial edge of Eb3; narrowly continuous mid-posteriorly with SOD.

OD3–4 origin broadly on Pb3 dorsally ventral to

TEb2; insertion broadly on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally broadly on posterior surface of Eb4 beginning ventral to LE4 and extending medially; ventrally on Cb5 dorsoposteriorly, joining small raphe ventrolaterally with Ad5.

Ad1–3 absent.

Ad4 dorsally broadly on Eb4 posteroventrolaterally, extending medially just under (anterior to) lateral edge of OP; ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint, meeting Ad5 attachment on Cb4.

Ad5 dorsally on Cb4 posterolaterally; ventrally on Cb5 dorsally mostly anterior to OP, joining raphe posteroventrally with ventromedial edge of OP.

SOD very fine.

RDs separated by space less than half diameter of one RD.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. Eb4 levator process present on only one side of smaller specimen, absent on both sides of larger specimen. ② Eb4 levator process present on one side, absent on other.

PRIACANTHIDAE

Heteropriacanthus cruentatus (Lacepède), USNM 319919, 63.3 mm; ② = USNM 141752, 88.0 mm.

Plate 115

Description.

LE1 on dorsoposterior edge of Eb1 well lateral to uncinat process, but not extending onto distal quarter of surface.

LE2 on mid-dorsoposterior edge of Eb2, insertion continuous posteriorly with ligament attaching Eb2 to mid-anterior edge of Eb3.

LE3 relatively small, on joined tips of Eb3 and Eb4 uncinat processes.

LE4 on dorsal edge of Eb4 levator process, insertion continuous ventrolaterally with ventromedial edge of CT sheet joining PP ventrally.

LP finely tendinously on Eb4 at lateralmost edge of LE4 insertion.

LI1 on dorsomedialmost end of Pb2.

LI2 on Pb3 dorsolaterally at articulation with medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 broad, wing-like, depressed centrally, with lateral margin of depression on each side represented by a surface raphe that gives rise to thick CT sheet attaching to skull; muscle attached antero- and ventromedianly between Pb3s to CT of pharyngeal roof; fibers of anterior two-thirds of muscle curve posterolaterally, those of posterior third more-or-less transverse, fibers fuse laterally as muscle narrows and extends onto Eb2, attaching to Eb2 dorsally anterolateral to LE2

insertion; muscle is not connected posteriorly with TPb3-Eb4. TPb3-Eb4 on Pb3 dorsoposterolaterally, extending broadly posteriorly onto medial arm of Eb4 anteriorly, attached mid-anteroventrally to CT of pharyngeal roof.

OD3-4, OD4v origin broadly on Pb3 dorsomedially ventral to TD, insertion on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process, with short, separate branch (OD4v, not illustrated) attaching broadly dorsally on Eb4 ventromedial to uncinat process.

Remarks. OD4v probably autapomorphic.

OP dorsally on Eb4 posteriorly, beginning on posterior surface of uncinat process and extending medially and becoming undifferentiated from SO, ventrally on Cb5 dorsoposterolaterally, ventrolaterally joining raphe with Ad5 posteroventrally.

Ad1-3 absent.

Ad4 dorsally broadly on Eb4 beginning on ventral surface of levator process and extending laterally on Eb4 posteriorly, ventrally on Cb4 dorsolaterally medial to Eb4-Cb4 joint.

Ad5 dorsally on Eb4 posterodistally, including tiny AC4 attached to posterodistal end of Cb4 (present on right and left arches), ventrally on Cb5 dorsally anterior to OP, joining raphe with OP ventrolaterally. ② AC absent.

Remarks. Presence of AC4 is variable, and possibly ontogenetically correlated. In a cleared and stained specimen 58.9 mm (USNM 337685) it is present on one side but not the other.

SOD absent.

RDs separated by space less than one RD diameter.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. IAC reduced to tiny cartilage adjacent to tip of Eb1 uncinat process, attached by long, slender ligament to tip of Pb2 uncinat process.

OSTRACOBERYCIDAE

Ostracoberyx dorygenys Fowler, USNM 307282, 80.0 mm.

Plate 116

Description.

LE1 broadly on dorsoposterior edge of Eb1 beginning on ventrolateral edge of long uncinat process and extending laterally; origin by long tendon.

LE2 very broadly on expanded posterior surface of Eb2, ventromedial edge of insertion meeting TEb2 posteriorly.

LE3 on joined tips of Eb3 and Eb4 uncinat processes anteriorly, muscously on Eb3, tendinously on Eb4.

LE4 broadly on Eb4 dorsolaterally, ventroposteromedially joining raphe with Ad4 dorsomedially

(present on both sides and can be characterized as an LE4-Ad4 muscle sling).

LP very slender, tendinously on dorsodistalmost edge of Eb4, joining ventrolateral edge of LE4 insertion.

LI1 on dorsalmost edge of Pb2, ventromedial edge of insertion joining raphe with TPb2 anterolaterally; muscle about same size as LI2.

LI2 on Pb3 dorsoposteriorly at medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 a thick, roundish pad broadly continuous ventrally with TEb2; attaching anteriorly to CT of pharyngeal roof; attaching tendinously anterolaterally to dorsal edge of Pb2 and adjacent anterior tip of Pb3 (not illustrated); with broad mid-dorsal raphe-like area giving rise to tough, filmy CT sheets covering TD. TEb2 extending laterally onto Eb2 anterior to LE2 insertion, continuous mid-ventroposteriorly by diagonal muscle strands with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsoposterolaterally near medial edge of LI2 insertion, rising dorsally onto Eb3 beginning on posteromedialmost edge and extending a short distance along posteriorly, continuous posteriorly with slender SOD.

OD3-4 origin on Pb3 dorsoanterolaterally ventral to TEb2, insertion broadly on Eb3 uncinat process anteriorly and medial edge of Eb4 uncinat process, joining narrow raphe posteroventrally with OP a little medial to Eb4 uncinat process.

OP dorsally broadly on Eb4 posteriorly beginning at uncinat process, extending medially, and becoming inseparable from SO, ventrally on Cb5 posterolaterally, joining short raphe with Ad5 ventrally.

Ad1-3 absent.

Ad4 on Eb4 dorsoposterolaterally and Cb4 dorsolaterally medial to Eb4-Cb4 joint, joining raphe with Ad5 dorsoanteriorly on Cb4.

Ad5 dorsally beginning tendinously on Cb4 posterodistally and extending medially on Cb4 dorsally, joining raphe with Ad4 ventrally; ventrally, narrowly on Cb5 dorsodistally, joining raphe with OP ventrally.

SOD moderately slender.

RDs separated by space equal to about one RD diameter.

Additional remarks. SCL attached mid-posteriorly to anterior surface of posteroventrally extending cartilage tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC present. Pb2 toothed. Eb4 levator process absent.

CIRRHITIDAE

Paracirrhites forsteri (Schneider), USNM 278070, 91.3 mm; USNM 339098, 67.2 mm.

Plate 117

Additional material. ② = *Cirrhitus pinnulatus* (Forster), USNM 296746, 65.0 mm.

Description.

LE1 broadly on Eb1 uncinat process anteriorly just lateral to cartilaginous tip; origin narrowly, tendinously united with posterior surface of epithelial sheet fronting gill arches dorsoanteriorly, separating them from pseudobranchs, also incorporates Pb1s. Strong ligament inserts on Eb1 anterior to LE1 and extends to cranium. ② Ligament and epithelial sheet possibly removed without notation (early dissection).

LE2 on Eb2 at about mid-length dorsoposteriorly.

LE3 finely on tip of Eb3 uncinat process anteriorly, meeting insertion of OD3–4 on Eb3.

LE4 on Eb4 dorsally beginning on tip of levator process and extending medially a short distance, joined laterally or anterolaterally by LP insertion.

LP relatively small, on Eb4 joining LE4 insertion laterally or anterolaterally, insertion continuous ventrolaterally with CT sheet (not illustrated) attaching to fourth and fifth arches and incorporating PP ventrally.

LI1 broadly on Pb2 dorsally beginning just posteroventral to dorsal tip; medial edge of muscle, dorsal to insertion, attaches to CT joining TPb2 anteriorly to Pb2 and posteromedial edge of IAC.

LI2 on Pb3 broadly posterolaterally opposite medial edge of Eb3, medial edge of insertion meeting TPb3 laterally.

TD comprising TPb2, TEb2, and TPb3. TPb2, large, flat, circular, almost completely covering mid-section of TEb2, with shallow notch mid-anteriorly and mid-posteriorly connected by mid-longitudinal raphe, which gives rise dorsally to thin sheets of CT and is joined mid-ventrally by TEb2; muscle attached anterolaterally by CT to closely approximated Pb1-Eb1 joint, IAC-Pb2 joint, and medial edge of LI1; attached mid-anteriorly and mid-ventroposteriorly to CT of pharyngeal roof. TEb2 medially ventral to TPb2, attaching along mid-longitudinal raphe ventrally, extending laterally and attaching on Eb2 dorsally a little anterolateral to LE2 insertion; posteriorly discontinuous from TPb3. TPb3 on Pb3 mostly ventral to OD3–4, attaching on Pb3 posterolaterally meeting medial edge of LI2 insertion, continuous by diagonal muscle strand with SOD. ② TPb2 on TEb2 dorsally; a flat, semicircular ribbon, open anteriorly, originating anteriorly on each side at CT attachment to closely approximated Pb1-Eb1 joint, IAC-Pb2 joint, and medial edge of LI1.

OD3–4 origin broadly on Pb3 medially ventral to TEb2, insertion on anterior surfaces of Eb3 and Eb4 uncinat processes.

OP dorsally, broadly on Eb4 beginning at medial end of bony portion and extending laterally almost to levator process, there meeting dorsomedial end of

Ad4; ventrally on Cb5 posterolaterally, variably joining or not short raphe with ventroposterior end of Ad5 and more extensive one with PCI.

M. SO-Pb3 originates from SO longitudinal muscle layer as two broad, anteriorly extending muscle straps, lateral strap inserts on Pb3 posteriorly, medial strap (not visible in illustration) originates ventral or ventromedial to RD and inserts on Pb3 posteromedially; RD inserts on Pb3 between M. SO-Pb3 pair.

Ad1–3 absent, but very fine muscle strand obscured by bases of gill-filaments on each arch anterolaterally.

Ad4 dorsally on Eb4 ventrally, beginning below levator process and extending to Eb4-Cb4 joint, ventrally, broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally, moderately broadly on posterolateral surface of Cb4, ventrally on Cb5 posterolaterally, variably joining or not OP posterolaterally in a short raphe.

SOD present.

RDs moderately separated or adjacent, insert by long tendon on Pb3 posteriorly between insertions of lateral and medial M. SO-Pb3 pair, except on one side of one specimen, in which RD tendon inserts into CT of pharyngeal roof posterior to Pb3.

Additional remarks. SCL attached mid-dorsally to posteroventrally elongated cartilaginous end of Bb3. TV4 free from Cb5s. Pb4, UP4, and IAC present. Pb1s oriented perpendicular to distal ends of Eb1s; ② Pb1s oriented parallel to Eb1s.

PEMPHERIDAE

Pempheris schomburgkii Müller and Troschel, USNM 318588, 95.5 mm; *Pempheris schwenkii* Bleeker, USNM 324224, 105 mm.

Plate 118

Additional material. ② = *Parapriacanthus ransonneti* Steindachner, USNM 344281, 79.2 mm.

GLAUCOSOMATIDAE

③ = *Glaucosoma magnificum*, WAM P14208-011, 93.2 mm.

Not illustrated

Remarks. We noted no substantive differences among the three genera.

Description (based on *Pempheris schomburgkii*).

LE1 relatively slender, on dorsal edge of Eb1 uncinat process just lateral to cartilaginous tip; strong, fine ligament (not illustrated) extends dorsally to ventral surface of the skull from margin of Eb1 anterior to uncinat process; ligament is appressed to posterior surface of vertical CT pane lining pharyngeal area anterior to gill arches.

LE2 on rounded high point of dorsoposterior edge of Eb2 mid-laterally.

LE3 on dorsal tip of Eb3 uncinat process.

LE4 on dorsodistal edge of Eb4, joining LP anteroventrally; levator process absent. ② LE4 and LP on levator process. ③ Levator process present.

LP on Eb4 at and anterior to LE4 insertion. ② ③ See LE4 above.

LI1 has long, slender tendinous insertion on Pb2 ventral to joint with IAC.

LI2 short tendinous insertion on Pb3 dorsoposterolateral surface at and just touching medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2, thick, pad-like, oblong, with irregular mid-longitudinal raphe giving rise to CT sheet covering muscle on anterior half; muscle attaches beginning anteriorly at CT of pharyngeal roof, continuing laterally over and attaching to anterior end of Pb3, dorsomedial surface of broad Pb2 uncinat process, and dorsomedial surface of IAC, remainder of muscle margin free, but muscle fusing ventromedially with TEb2; amorphous CT connects mid-posteroventral surface to mid-anterior edge of TPb3-Eb3. TEb2 extending out on dorsal surface of Eb2 to point anterolateral to LE2 insertion. TPb3-Eb3 on Pb3 posterolaterally, continuing on Eb3 posteromedial edge, continuous ventrally by crossing strands of muscle with SOD, which is ventral to TPb3-Eb3. ② TPb2 flat, attachment on IAC extends to about mid-length of element. ③ Attachment extends laterally only to dorsolateral-most edge of Pb2 (i.e., not on IAC).

OD3–4 origin on Pb3 ventral to TPb2 and TEb2, inserting on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally on Eb4 mid-dorsoposteriorly beginning at uncinat process and continuing medially about half distance to medial end of Eb4, extending ventrally posterior to dorsomedial edge of Ad4 and posteroventral surface of Ad5 and inserting on posterodistal surface of Cb5.

Ad1–3 absent.

Ad4 dorsally on ventral surface of Eb4 mostly lateral to OP, and ventrally, broadly on Cb4 dorsal surface medial to Eb4-Cb4 joint.

Ad5 ventrally on dorsal surface of distal end of Cb5 anterior to OP insertion and broadly on Cb4 ventroposterior surface and small AC4 posteriorly.

SOD slender, ventral to TPb3-Eb3; moderately well developed, just ventroposterior to TPb3-Eb3 in *P. schwenkii*. ② Well-developed, well posterior to TPb3-Eb3, but continuous with it by slender, diagonal muscle strap. ③ Very fine, ventral to TPb3-Eb3.

RDs adjacent.

Additional remarks. SCL present, attached mid-dorsally by long, loose CT to tip of elongate, ventroposteriorly extending cartilaginous posterior end of

Bb3. TV4 free from Cb5s. ② SCL apparently free from short, cartilaginous posterior end of Bb3 (should be verified in additional specimens). Pb4 and UP4 present. Pb2 toothed.

Johnson (1993:19), following Tominaga (1986), recommended recognizing the Glaucosomatidae as a subfamily of the Pempheridae and described additional specializations shared by the two groups. Nelson (1994:365–366), McKay (1997:5), and Mooi and Gill (2002:23), without explanation, all chose not to follow Johnson's recommendation. McKay (1997:5) proposed that the Pempheridae and Glaucosomatidae are sister groups.

To the specializations shared by pempherids and glaucosomatids previously reported in the literature, we add the ligament positioned anterior to LE1, a general similarity of the dorsal gill-arch musculature, and the shape of Eb4, which is posteriorly concave.

LACTARIIDAE

Lactarius lactarius (Bloch and Schneider), USNM 343873, 119 mm.

Plate 119

Description.

LE1 on Eb1 uncinat process ventrolateral to tip; origin tendinous; long, broad-based ligament on Eb1 anterior to uncinat process (also in *Glaucosoma*—see additional remarks under Pempheridae).

LE2 on dorsally expanded bony posterior margin of Eb2.

LE3 on tip of Eb3 uncinat process medially.

LE4 on Eb4 levator process beginning at ventrally positioned cartilage tip and extending medially.

LP on Eb4 at and anterior to anterior margin of LE4 insertion, ventrolaterally joining CT sheet.

LI1 very broad dorsally, on Pb2 dorsally, medially ventral to TPb2.

LI2 on Pb3 dorsoposterolaterally just anterior to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 heart-shaped, attaching to Pb2 dorsoanteriorly, with median longitudinal raphe posteriorly; raphe joined ventrally by TEb2 medially. TEb2 broad, attaching along mid-longitudinal raphe ventrally between Pb3s with CT of pharyngeal roof, narrowing laterally and attaching along Eb2 dorsally anterior to LE2 insertion, continuous mid-posteriorly by CT (not illustrated) with TPb3-Eb3 mid-anteriorly. TPb3-Eb3 on Pb3 dorsoposterolaterally medial to medial end of Eb3 and on posteromedial edge of Eb3, continuous posteriorly by diagonal muscle strands with SOD.

OD3–4 origin on Pb3 dorsoanteromedially ventral to TEb2; insertion on anterior surface of Eb3 uncinat process and medial edge of Eb4.

OP dorsally on Eb4 posteriorly at and medial to

uncinate process; ventrally on Cb5 posterodistally, joining raphe ventrolaterally with Ad5.

Ad1–3 absent.

Ad4 dorsally broadly on Eb4 posteriorly beginning ventrally at levator process and extending laterally to end of bone, ventrally broadly on Cb4 dorsally medial to Eb4–Cb4 joint, meeting Ad5 anterolaterally on Cb4, but diverging from Ad5 medially.

Ad5 dorsally on Cb4 bony surface entirely medial to cartilaginous end; ventrally on Cb5 dorsolaterally joining raphe posterolaterally with OP.

SOD slender.

RDs separated by space greater than one RD diameter.

Additional remarks. SCL attached mid-dorsally to tip of posteroventrally extending cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC present.

LATEOLABRACIDAE²

Lateolabrax japonicus (Cuvier), USNM 344295, ② = 102 mm; USNM 64631, 109 mm.

Plate 120

Description.

LE1 on bony anterior surface of Eb1 uncinat process.

LE2 on dorsomedial edge of expanded bony edge of Eb2.

LE3 on joined tips of Eb3 and Eb4 uncinat processes, there joining raphe with OD3–4 insertion.

LE4 on Eb4 dorsal surface lateral to uncinat process.

LP on Eb4 at and lateral to LE4 insertion.

LI1 on most of dorsal surface of Pb2; with few anterolateral fibers on anteromedial surface of IAC on one side and extensive attachment to medial surface of IAC on other.

LI2 on Pb3 dorsal surface posterolaterally, beginning anteriorly a little anterior to articulation with medial end of Eb3 and extending posteriorly to opposite to medial end anterior to attachment of TPb3–Pb4–Eb3 to Eb3.

TD comprises TEb2 and TPb3–Pb4–Eb3. TEb2 with median longitudinal raphe, which gives rise dorsally to CT sheets covering muscles and attaches mid-anteroventrally to CT of pharyngeal roof and to CT enveloping (attaching to) anterior ends of Pb3s; muscle attaching along Eb2 dorsally to area anterior to LE2 insertion, continuing posteriorly by diagonal

² The familial placement of *Lateolabrax* is problematic. It has been variously assigned to *Percoidei insertae sedis* (Johnson, 1984: 465) or *Percichthyidae* (Mochizuki, 1984:123). Springer and Raasch (1995:94, 104) assigned it to *Lateolabracidae*, which appears to be the first published usage of a family name based on the genus. The name appeared next in Orrell et al. (2002:628).

strand of muscle with TPb3–Pb4–Eb3. TPb3–Pb4–Eb3 attaching laterally on dorsal surface of Pb3, dorsoanterior edge of Pb4, and posteromedialmost surface of Eb3, continuing posteriorly by crossing strands of muscle with SOD.

OD3–4 origin broadly on Pb3 dorsomedially ventral to TEb2, insertion on anterior surface of Eb3 uncinat process, dorsal to OD3', and on medial edge of Eb4 uncinat process.

OD3' branches off OD3–4 anteroventrally just posterior to OD3–4's passing out posteriorly from under TEb2 and inserting on Eb3 dorsal surface ventral to OD3–4 insertion on uncinat process.

OP dorsally on bony posterior surface of Eb4 medial to uncinat process, dorsolaterally overlapping Ad4 dorsomedially, ventrally on Cb5 posterodistally, partially overlapping Ad5 ventromedially.

Ad1–3 absent.

Ad4 dorsally on posterior surface of Eb4 lateral to OP, ventrally on Cb4 anterior to Eb4–Cb4 joint.

Ad5 dorsally on posterodistal surface of Cb4, ventrally on dorsodistal surface of Cb5 anterior to OP.

SOD present.

RDs narrowly separated.

Additional remarks. SCL attached mid-dorsally to ventroposterior cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Levator process present on posterior edge of right-side Eb4, not present on left side; present on both sides of ② and of cleared and stained specimen, USNM 177447.

SCIAENIDAE

Cynoscion nebulosus (Cuvier), USNM 176237, 76.8 mm.

Plate 121

Additional material. *Cynoscion arenarius* Ginsburg, USNM 120047, 117 mm.

Remarks. We noted no significant differences between the muscles of *C. arenarius* and *C. nebulosus*, except that SOD in the former is strap-like and normal.

Description.

LE1 short, with tendinous origin, insertion broadly on anterior surface of Eb1 uncinat process.

LE2 on expanded bony dorsoposterior surface of Eb2.

LE3 on Eb3 uncinat process dorsally and dorsal edge of Eb4 uncinat process just medial to cartilage tip.

LE4 on Eb4 dorsally beginning lateral to uncinat process and extending to cartilaginous distal edge.

LP on LE4 at and just anterior to LE4 insertion.

LI1 on dorsomedialmost surface of IAC, continuing onto adjacent surface of Pb2, and extending to

CT that binds anteriormost ends of Pb2 and Pb3; much larger than LI2.

LI2 on dorsolateral surface of Pb3 just anterior to anteromedial end of Eb3.

TD comprises TEb2 and TPb3-Eb3. TEb2 with mid-longitudinal raphe giving rise dorsally to filmy CT covering muscle, attached anteriorly and mid-ventrally to CT of pharyngeal roof and laterally on dorsal surface of Eb2 to point anterior to LE2 insertion, continuing posteroventrally by fine, diagonal muscle strand with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsolaterally posteromedial to LI2 insertion, and on Eb3 dorsoposteromedial surface, passing freely over medial end of Eb4 before attaching to Eb3, posteriorly continuous by fine diagonal muscle strand with very fine SOD.

OD3–4 origin on Pb3 dorsoanteriorly ventral to TEb2, insertion on anterior surface of Eb3 uncinat process, joining raphe with anteroventral edge of LE3 insertion, and on anterior surface of Eb4 uncinat process.

OP dorsally on Eb4 posterior surface extending medially beginning ventral to uncinat process, ventrally beginning on Cb5 posterior surface distally, there joining broad raphe with PCI and extending medially; distinctly separate from Ad4 and SO.

Ad1–3 absent.

Ad4 dorsally on Eb4 posterior surface extending laterally beginning from point ventral to LE4 and LP insertions, ventrally on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 on posterodistal end of Cb4 and dorsodistal end of Cb5, forming short raphe at that point with PCI and Ad4.

SOD very fine, aberrant, passes dorsal to RD of left side and returns to SO between RDs. ② Strap-like, continuous from one side to the other.

RDs well separated.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. Eb4 levator process absent.

Sasaki (1989) described and illustrated in detail the dorsal gill-arch musculature of *Ctenosciaena gracilicirrhus* (Metzelaar), with which *Cynoscion* agrees. Sasaki did not detail the attachments of his transversus dorsalis posterior, but his illustration (his fig. 37) conveys the impression that it is TPb3-Eb3, similar to that of *Cynoscion*. Sasaki also described and illustrated (his figs. 42, 44) differences shown by *Pogonius*, *Aplodinodus*, and *Leiostomus*, highly specialized western Atlantic and/or freshwater inhabitants. The differences shown by these three genera mainly involve an interrupted TEb2; broad, muscously naked Pb3 dorsal facets; and an unusually well-developed Ad5.

The insertion of LI1 to include IAC is uncommon. It also occurs in haemulids and bathyclupeids, both

of which also share with *Cynoscion* the specialized state of lacking SCL, and in bramids, kuhliids, and lateolabracids, which have SCL.

POLYNEMIDAE

Polydactylus oligodon (Günther), USNM 364370, 128 mm.

Plate 122

Additional material. ② = *Filimanus xanthonema* (Valenciennes), USNM 278199, 99.1 mm.

Description.

Remarks. LE1–4 insertions muscous and tendinous (tendinous portions not illustrated).

LE1 on Eb1 just lateral to tip of uncinat process.

LE2 on tip of bony process on proximal half of posterior edge of Eb2.

LE3 on anterior edge of tip of Eb3 uncinat process.

LE4 on bony dorsal edge of Eb4 lateral to tip of uncinat process.

LP on Eb4 beginning at lateral edge of LE4.

LI1 tendinously on Pb2 dorsally posteroventral to Pb2 articulation with IAC with tendon continuing onto adjacent dorsoanterior end of Pb3. ② Muscle fibers reach lateral edge of Pb3.

LI2 on Pb3 dorsolaterally just medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 flat, roughly kidney-shaped, in two sections; triangular small anterior section fitting into mid-anterior notch of much larger posterior section; posterior section with mid-longitudinal raphe continuous posteriorly through TEb2; raphe giving rise dorsally to CT sheets attaching to skull; raphe continuous mid-ventrally with CT of pharyngeal roof; muscle attaching anterolaterally to Pb2 just medial to dorsoanteriormost cartilaginous tip and joining ventrally to TEb2 lateral to raphe. TEb2 anterior fibers extending laterally and passing dorsoposterior to posterior fibers and both portions attaching dorsally a short distance lateral to medial end of Eb2, posteriormost fibers continue finely tendinously dorsoanteriorly over other TEb2 fibers and attach to IAC; muscle continuous posteriorly by diagonal strip of muscle with TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 on Pb3 dorsolaterally, partly joining posteromedial edge of LI2 insertion, continuing posteriorly medial to posteromedial end of Eb3 and attaching tendinously to it, next continuing onto Pb4 dorsolaterally medial to medial end of Eb4, then continuing posteriorly by diagonal muscle strap with SOD. ② Anterior section of TPb2 is continuous posteriorly with TEb2 ventral to posterior section, hence, is part of TEb2.

OD3–4 robust, origin broadly on Pb3 dorsomedially mostly ventral to TEb2, but partially posterior to

TEb2; posteriorly on medial edge of Eb3 uncinat process and anterior surface and medial edge of Eb4 uncinat process, joining raphe with OP dorsally medial to tip of Eb4 uncinat process (raphe longer on right side). ② No raphe with OP.

OP dorsally beginning on Pb4 posterolaterally and extending laterally onto Eb4 posteriorly to point slightly ventrolateral to uncinat process, there joining tendon on Eb4 with dorsomedial end of Ad4 (tendon and associated CT sheets continue to cleithrum, with long tendinous attachment of PP to CT among sheets ventral to Eb4—only tendon illustrated); ventrally on Cb5 ventrolaterally posterior to Ad5, joining raphe with Ad5 posterolateralmost edge; mid-medially confluent with SO. ② No fibers on Pb4.

Remarks. Fibers on Pb4 possibly more appropriately allocated to SO.

Ad1–3 absent, but frayed fan-like GFM on Eb1–Cb1 joint anteriorly.

Ad4 dorsally on Eb4 ventrally mostly lateral to OP, ventrally on Cb4 medial to Eb4–Cb4 joint, joining raphe ventroposteriorly with Ad5.

Ad5 dorsally on Cb4 posterolaterally, anteriorly joining raphe with Ad4.

SOD present.

RDs adjacent.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Pb1 with cartilaginous ends. Pb2 toothed. Eb4 levator process absent.

SILLAGINIDAE

Sillago sihama (Forsskål), USNM 347113, 139 mm.

Plate 123

Description.

LE1 narrowly on tip of small bony process extending anteriorly from just below cartilage tip of Eb1 uncinat process, muscle fanning out dorsally.

LE2 narrowly on small bony process on Eb2 dorso posteriorly, muscle expanding dorsally.

LE3 on Eb3 uncinat process anteriorly, ventroanteriorly joining OD3–4 on Eb3.

LE4 on Eb4 dorsolaterally near distal end, joined ventrolaterally by LP.

LP on dorsodistalmost surface of Eb4, joining LE4 insertion ventrolaterally.

LI1 thin, strap-like, on dorsoanterolateralmost surface of Pb2 and dorsomedial surface of IAC, just impinging on fine tendinous origin of M. Pb2–Eb2, ventral half and dorsal fourth muscular, separated by band of clear CT lying against LE2 medially (areas of CT and adjacent LE2 about equal).

LI2 on Pb3 dorsolaterally medial to articulation with Eb3, medial edge of insertion meets anterolateral edge of TPb3–Eb3.

TD comprises TPb2, TEb2, and TPb3–Eb3. TPb2 roughly heart-shaped, notched mid-anteriorly, with

deep mid-longitudinal raphe, which attaches ventrally to CT of pharyngeal roof, extending posteriorly from notch and continuing across ventrally lying TEb2 broad portion, which attaches dorsally to TPb2 along raphe; raphe thence continuing across dorsal TEb2 narrow portion, becoming tendinous strand and continuing across TPb3–Eb3 and anterior half of SOD; anterolaterally, TPb2 attaches to Pb2 dorsoanteriorly medial to origin of M. Pb2–Eb2. TEb2 comprising two incompletely separated parts: broad anterior part, which lies mostly ventral to TPb2, and narrow posterior part, which is external; anterior part attenuating laterally, passing ventral to M. Pb2–Eb2 and meshing with it as they extend almost to distal end of Eb2 bony surface, there meeting Ad2 posteromedially; posterior part narrows considerably laterally and attaches to medial edge of bony process bearing LE2 insertion (some fibers from anterior TEb2 part also attach to this edge). TPb3–Eb3 not continuous muscously with TEb2, almost completely occluded from view by overlying OD3 and OD4; muscle curves anterolaterally dividing into ventral branch, which attaches to Pb3 beginning at medial edge of LI2 insertion and continuing posteriorly to bony edge bordering articulation with Pb4 and Eb4, and dorsal branch, which passes dorsal to medial end of Eb4 and attaches to posterior edge of medial half of Eb3. (See also M. Pb2–Eb2.)

OD3, OD3', OD4, essentially separate muscles. OD4 robust, originating on Pb3 dorsomedially, overlying much of posterior half of OD3, and inserting on medial edge of uncinat process and much of posterior surface of Eb4, meeting LE4 and LP insertions. OD3 robust, originating on Pb3 just ventrolateral to OD4 and inserting on most of bony anterior surface of Eb3 uncinat process, meeting LE3 insertion ventrally and slightly separated dorsally from distal end of OD3'. OD3 and OD4 fibers mingle at tightly joined Eb3 and Eb4 uncinat processes. OD3' slender, originating on Pb3 ventral to OD3 and inserting a little more than halfway distally on Eb3 dorso posteriorly, there meeting Ad3.

OP with two sections: medial section broadly dorsally on Eb4 posteriorly beginning at medial end of bony surface and extending laterally to near LP–LE4 insertions, laterally overlapping dorsomedial half of lateral section; lateral section beginning on Eb4 posteroventrally (anterior to medial section), extending dorsolaterally and attaining same attachment level as medial section, and ending laterally at distal end of bony surface. Medial section broadly ventrally on entire posterior surface of lateral arm (horn) of Cb5; lateral section narrowly distally on horn, meeting OP distally, and both meeting Ad5 posteroventrally. OP completely occludes Ad4 in posterior view.

M. Pb2–Eb2 relatively large, originating finely, tendinously on Pb2 dorsoanteriorly with and medial

to TPb2 insertion and extending posterolaterally onto Eb2 almost to distal end of dorsal bony surface, lying dorsal to TEb2 as it extends onto Eb2 and meshing ventrally with TEb2, meeting medial end of Ad2 posteriorly.

Ad1 absent, weak GFM filaments on anterodistal surfaces of Eb1 and Cb1.

Ad2 small, extending from dorsodistal surface of Eb2 to anterodistal surface of Cb2, meeting distal end of M. Pb2-Eb2.

Ad3 extending laterally from anteromedialmost bony surface of Eb3 to anterodistal surface of Cb3, meeting anterodistal end of OD3'.

Ad4 ventrally on Eb4 anterior to lateral OP section, ventrally broadly on Cb4 anterior to Eb4-Cb4 joint, posteriorly excluded from view by OP.

Ad5 bulky, dorsally relatively broadly on posterodistal surface of Cb4, there meeting distal three-fourths of Ad4 attachment posteriorly, ventrally on Cb5 dorsodistally, passing anterior to OP lateral section.

SOD present.

RDs adjacent; together forming cup-shaped depression dorsally.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Tiny AC2 present on both sides (also on both sides of C&S specimen, USNM 269802). Eb4 levator process absent. Broad bony flange overlapping cartilaginous distal end of Eb4 anteriorly.

MULLIDAE

Pseudupeneus maculatus (Bloch), USNM 267508, 2 specimens, 94.0–116 mm.

Plate 124

Additional material. ② = *Parupeneus multifasciatus* (Quoy and Gaimard), USNM 267485, 2 specimens, 80.0–99.7 mm.

Description.

Remarks. We observed no noteworthy differences between any of the specimens.

LE1 on dorsoanterior surface of Eb1 uncinat process.

LE2 on dorsal tip of expanded bony posterior edge of Eb2.

LE3 tendinously on tightly bound tips of Eb3 and Eb4 uncinat processes.

LE4 on dorsoposterior edge of Eb4.

LP on Eb4 at and lateral to lateral edge of LE4 insertion.

L11 on Pb2 ventral to tip of dorsoanterior process.

L12 on Pb3 dorsoposteriorly just medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 consists of an anterior transverse strip of muscle at-

taching to each IAC dorsolaterally and continuing mid-posteriorly with TEb2 and slightly laterally with pair of slender, laterally convex ribbons of muscle lying dorsal to TEb2; each ribbon with mid-lateral raphe and fusing anteriorly and posteriorly with TEb2 lateral to mid-longitudinal raphe, which extends continuously from anterior end of TD almost to posterior edge of TPb3-Eb3; mid-longitudinal raphe attached ventroanteromedially to CT of pharyngeal roof and giving rise dorsally to CT sheets that cover muscle and attach to skull. TEb2 extensive, attaching on dorsal surface of Eb2 laterally anterior to LE2 insertion, posteriorly continuous (or free, variable in specimens) by strands of muscle with TPb3-Eb3. TPb3-Eb3 beginning anteriorly on Pb3 dorsally just medial to medial end of Eb3 and continuing posteriorly and abruptly expanding greatly laterally and attaching on Eb3 dorsomedially; continuous by diagonal strands of muscle with SOD.

OD3–4, OD3' origin on Pb3 ventral to TEb2, dividing ventrally (OD3') just before inserting on dorsoanterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process; OD3' insertion on Eb3 dorsal surface just ventral to Eb3 portion of OD3–4.

OP dorsally broadly on Eb4 posterior surface ventromedial to insertions of LE4-LP, ventrally on dorsoanterior edge of Cb5.

Ad1–3 absent.

Ad4 dorsally broadly on Eb4 posterior surface lateral to OP, ventrally on Cb4 dorsal surface medial to Eb4-Cb4 joint.

Ad5 on dorsodistal surface of Cb5 and posterodistal end of Cb4 and Eb4.

SOD present.

RDs separate.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 and Pb4 absent, UP4 present. Eb4 levator process absent; however, darkly blue-stained area near posterior point of LP insertion seems to indicate that a cartilage tip may have been present early in ontogeny. AC2 (not illustrated) present on both sides of one specimen but absent on both sides of other specimen; additionally, AC2 present on both sides of two specimens of *Mulloidides flavolineatus* (USNM 272965, cleared and stained). ② No ACs present in either specimen.

Kim (2002:35–36) briefly described and diagrammatically illustrated the dorsal gill-arch muscles of *Upeneus vittatus* Forsskal, a member of the genus he hypothesized as the sister-group to all the other mullid genera. Although he describes TPb2 as including IAC among its attachments, his illustration of TPb2 does not exhibit the anterolateral extensions of the muscle that attach to IAC that are present in our specimens of *Parupeneus* and *Pseudupeneus*.

CENTROGENIIDAE

Centrogenys vaigiensis (Quoy and Gaimard), USNM 183016, 84.7 mm; ② = USNM 327899, 93.5 mm.

Plate 125

Description.

Remarks. The musculature of *Centrogenys* is unusually bulky and invested with tough CT, relative to the small size of the specimens. Determinations of extent and attachments of TD, OD, OP, and Ad4 & 5 are particularly difficult and require considerable destruction of muscles.

LE1 on Eb1 uncinat process lateral to tip.

LE2 on mid-dorsoposterior edge of Eb2 almost touching TEb2 posteriorly.

LE3 broadly dorsally on and lateral to tip of Eb3 uncinat process and narrowly on dorsal tip of bony Eb4 uncinat process.

LE4 massive, on Eb4 broadly dorsoposteriorly lateral to all bony uncinat process (see remarks following OD3–4) and anterior to levator process, joining raphe posteroventromedially with OP dorsally. ② Raphe more extensive in larger specimen.

LP on Eb4 dorsoposterior margin medial to minute cartilage tip of levator process, joining raphe with LE4 insertion posterolaterally; finely continuous ventrolaterally with OP in ②, but ignored in coding character for matrix (Table 12, Appendix).

LI1 on dorsalmost edge of Pb2 and dorsoanterior surface of Pb3 posterior to anterior end (Pb2 edentate, much reduced and closely applied medially to lateral surface of Pb3).

LI2 on Pb3 dorsoposteriorly medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3 (see also ②). TPb2 bun-like muscle pad on each side continuous with each other medially by tough, thick, broad fascia, which gives rise to tough CT sheets attaching to skull; muscle dorsal to medial ends of bilaterally divided TEb2, attaches to dorsoanterior ends of Pb2 and Pb3 and, between Pbs to CT of pharyngeal roof; muscle coverage mostly absent from dorsal Pb3 surface. TEb2 a muscle pair, each member becoming tendinous medially and dorsally joining ventral midline CT between Pbs, muscle extending onto Eb2 dorsally well lateral to LE2 insertion. TPb3 on Pb3 posterolaterally medial to medial end of Eb4, continuous posteriorly by diagonal muscle filament with SOD. ② Comprises TPb2, TEb2, and TPb3-Pb4.

OD3–4 massive, origin tendinous, on Pb3 anterolaterally ventral to TEb2, there joining fascia of TPb2 and TEb2; insertion extensively on Eb3 dorsoanteriorly and on medial edge of Eb4 bony uncinat process, continuing onto posterior surface of process.

Remarks. In the described smaller specimen, the Eb4 uncinat process bears an easily overlooked tiny cartilage tip (absent in the larger specimen) ventral

to the more dorsal bony surface that is tightly joined to the Eb3 uncinat process. The tip is visible only by severing the CT joining the two processes. It appears that the cartilage tip is lost with growth, and its absence is considered typical for the taxon.

OP complex, bulky, possibly representing a fusion of primitively mostly separate lateral and medial sections; dorsally attached to most of broad ventral Eb4 surface anterior to Ad4, dorsoposteriorly joining raphe with LE4 ventroposteromedially, ventrolaterally becoming tendinous and joined laterally by Ad5 and ventrally by PCI, ventrolaterally broadly on Cb5 posterolaterally, joining raphe with PCI anterolaterally and TV5 anterolaterally, continuous medially with SO. ② Raphe with LE4 more extensive.

Ad1–3 absent.

Ad4 broadly dorsally on ventral Eb4 surface posterior to OP, ventrally broadly on Cb4 paralleling Ad5 attachment medial to Eb4-Cb4 joint.

Ad5 dorsally broadly on posterolateral surface of Cb4 and AC, ventrally broadly on Cb5 posteriorly, joining raphe with PCI dorsoanteriorly and OP tendon anteromedially.

SOD present.

RDs adjacent.

Additional remarks. SCL free from Bb3. TV4 ventrally continuous across ventral surface of Cb5s, dorsally interrupted, attaching to anterolateral surface of each Cb5. Pb4 and UP4 present. Pb2 edentate. IAC present. AC4 present.

Cb5s are tightly bound medially along sinuous joint, one side is larger than other and overlaps the smaller side dorsoanteriorly. The bones are not fused in specimens of the sizes we examined, but it seems likely that they might be in much larger specimens (species variously reported to attain a length of 150 or 200 mm).

AMBASSIDAE

Tetracentrum caudovittatus (Norman), USNM 332862, 74.1 mm.

Plate 126

Additional material. ② = *Ambassis buruensis*, USNM 305331, 55.0 mm.

Description.

LE1 on Eb1 uncinat process dorsoanteriorly just lateral to cartilage tip. ② On uncinat process just anteroventral to tip.

LE2 on dorsalmost edge of raised posterior surface of Eb2.

LE3 on medial edge of cartilage tip of Eb3 uncinat process. ② On tip of process dorsally.

LE4 massive; on dorsolateral surface of Eb4 reaching to lateralmost bony edge, there narrowly joining with anterolateralmost edge of LP; posteriorly, nar-

rowly, musculously continuous with OP dorsolaterally, just medial to posteromedial edge of LP insertion. ② Not continuous with OP.

LP little less robust than LE4; on Eb4 dorsally near distal bony end, ventroanteriorly joining LE4, meeting OP dorsolaterally. ② Slender, on dorsodistalmost bony edge of Eb4, ventromedially joining LE4.

LI1 passing between acute, laterally open angle formed by TPb2 with TEb2, and inserting by slender tendon on Pb2 dorsally beginning just ventral to medial end of broad cartilaginous cap, tendon joins CT extending onto adjacent bony surface of Pb3 just posterior to dorsoanteriormost cartilage tip.

LI2 on Pb3 dorsoposterolaterally adjacent to articulation with medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 moderately robust, with shallow notch mid-anteriorly leading to short, fine, mid-longitudinal septum. Septum posteriorly joins broad, oblong, thick, tough CT area, representing non-muscular mid-portion of TEb2 covering flat, dorsal Pb3 surfaces and attaching mid-ventrally to CT of pharyngeal roof; CT sheets arise from margins of oblong CT area and cover TPb2 and TEb2. TPb2 entirely anterior to TEb2, but joining oblong CT area anteriorly at point just anterior to anteromedialmost muscular portion of TEb2, there forming angle that embraces LI1 tendinous portion dorsal to insertion. TPb2 musculously on IAC beginning about mid-dorsally and extending medially onto Pb2 anteriorly a little medial to joint with IAC (② begins on IAC dorsomedially close to joint with Pb2); muscle is continuous across dorsal and anterior surfaces of Pb2s. CT area of TEb2 more extensive than TPb2; muscular TEb2 portion robust, but narrowing considerably as it extends onto Eb2, first dorsally, then anteriorly, reaching point anterolateral to LE2 insertion and meeting medial end of GFM2. TEb2 not continuous posteriorly with TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 beginning anteriorly, tendinously on posteromedial edge of Eb3 and adjacent surface of Pb3 and extending posteriorly on Pb4 dorsally parallel to medial end of Eb4 (superficially muscle appears to attach to medial end of Eb4). ② TPb3-Eb3 attaches to Pb3 (Pb4 absent) only on surface immediately medial to medial corner of Eb3.

M. SO-Pb3 (not visible in dorsal view) arises on each side as anteriorly extending slender ribbon of SO longitudinal fibers that inserts on Pb3 just ventroposterior to raised dorsoposterior surface.

OD3-4 robust, anteriorly ventral to TEb2 on transverse posterior edge of raised anterior half of Pb3, posteriorly, broadly on Eb3 uncinat process anteriorly and Eb4 uncinat process posteriorly, joining narrow raphe with OP on Eb4 medial to tip of Eb4 uncinat process.

OP in two or 3 irregular and almost completely separate sections, attaching dorsally along most of

posterior bony surface of Eb4; medial section beginning at uncinat process and extending medially, middle section beginning at lateral end of medial section and extending to area ventral to LP, lateral section beginning at lateral end of medial section and extending laterally almost to end of Eb4; lateralmost section narrowly, musculously continuous with LE4 (q.v.); lateralmost section ventrally on Cb5 posteriorly and dorsally, overlapping Ad5 posteriorly; other two sections more medially on Cb5. ② Not continuous with LE4, in two or three separate sections, lateralmost section either absent or fused ventrally with Ad5, q.v.

Ad1-3 absent. GFM1 fine on anterior surface of Eb1 and Cb1 at and near joint. GFM2 better developed, extending onto Eb2 anteriorly to about mid-length and meeting lateral end of TEb2; GFM3 well developed but limited to Eb3 dorsolaterally.

Ad4 dorsally, narrowly on Eb4 posteroventrally near angle with Cb4; ventrally, narrowly on Cb4 dorsally near angle with Eb4; completely overlapped posteriorly by OP and not visible in posterior or lateral views (distal ends of Cb4 and Cb5 unusually closely and tightly bound together).

Ad5 dorsally on Cb4 posterolaterally, ventrally on Cb5 dorsolaterally, including surface of dorsodistal bony flange; muscle extends medially on Cb5 a short distance anterior to OP. ② Ad5 appears to have fused with the lateralmost part of OP, or else has been lost, such that a single muscle representing one or both, OP or Ad5, extends from the dorsolateralmost end of Cb5 to Eb4.

SOD absent.

RDs massive, adjacent.

Additional remarks. SCL attached to ventrally extending cartilaginous posterior tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. (② Pb4 absent, UP4 present). Eb4 levator process absent. Very tiny AC3 present unilaterally (② no ACs present, but see discussion of ACs in section "Abbreviations and Definitions for Anatomical Structures" for *Ambassis* sp. with AC4). Bony flange of Eb4 projects laterally dorsal to cartilaginous distal end. Diameter of medial end of Eb3 greater than that of Eb4. ② Slightly less than diameter of Eb4; however, in two cleared and stained specimens, one each as *Ambassis macleayi*, USNM 173817, and *Ambassis* sp., USNM 218805, the medial end of Eb3 is slightly larger than that of Eb4. The medial end of Eb4 is treated as smaller than that of Eb3. Anterior end of Cb5 on one side overlaps anterior end on other side.

CARISTIIDAE

Caristius maderensis Maul, USNM 206895, 114 mm.

Plate 127

Description.

LE1 on dorsal edge of Eb1 just lateral to cartilage tip of well-developed uncinat process, which is well removed laterally from direct contact with anterior end of Eb1.

LE2 on Eb2 mid-dorsoposteriorly.

LE3 finely, tendinously on tip of Eb3 uncinat process medially.

LE4 origin tendinous; left side, tendinously on lateral surface of tip of Eb4 uncinat process; right side, similar to left side, but separate strip of muscle fibers extends onto bony edge of Eb4 ventrolateral to tip of uncinat process; ventrolateral edge of insertion meets ventroanterior edge of LP and together they are membranously continuous with Ad4 dorsally (see also LP).

LP origin tendinous; insertion joins ventrolateral edge of LE4 insertion and extends short distance laterally; LP and LE4 insertions join CT, which is joined ventrally by dorsoposterior end of medial Ad4 section, and the three muscles can be easily released as a cohesive group from Eb4. Broad CT sheet, which attaches to lateral edges of 4th and 5th arches, attaches medially to lateralmost edge of LP insertion.

LI1 on bony surface of Pb2 dorsoanteriorly beginning just ventral to dorsalmost cartilaginous tip.

LI2 on bony surface of Pb3 dorsoanteriorly just ventral to cartilaginous process articulating with medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 thick, roundish pad, depressed centrally, inseparable ventrally from TEb2; with pair of longitudinal raphe that give rise to CT sheets covering muscle and attaching to skull; CT also arising from dorsoposterior half of pad perimeter, beginning at mid-lateral raphe on each side, which is also joined ventrally by TEb2 medially (TPb2 and TEb2 inseparable medial to raphe); weak, tendinous strand extends anteriorly from mid-lateral raphe and attaches to Pb2 dorsolaterally; weak, filmy CT attaches muscle mid-ventrally between Pb3s to CT of pharyngeal roof. TEb2 extends laterally and attaches on Eb2 dorsally well lateral to LE2 insertion; diagonal muscle strand extending from posteroventral surface is continuous with Pb3 portion of TPb3-Eb3. TPb3-Eb3 on Pb3 dorsolaterally beginning medial to LI2 insertion and continuing posteriorly with laterally separate muscle strands attaching to cartilaginous medial end of Eb3 dorsally and posterior bony edge of Eb3; ventral diagonal muscle strands continuous with SOD.

Remarks. Vertical rotation of RDs has probably resulted in TPb3-Eb3 and SOD also becoming almost vertical (see also remarks following OD3-4).

OD3-4 origin on Pb3 dorsoanteromedially ventral to TPb2 and TEb2; muscle divides posteriorly with anterior branch inserting broadly on anterior surface of Eb3 beginning on uncinat process and extending

laterally, posterior branch inserting equally broadly on anterior surface of Eb4; most of Eb4 insertion is hidden from view.

OP dorsally on Eb4 posteriorly beginning medial to cartilage tip of uncinat process and extending medially with several medialmost fibers extending well anteriorly and inserting on Pb4 posteriorly; ventrally on Cb5 dorsoposterolaterally, posterior to Ad5 attachment, just joining raphe with Ad5 posterodistally.

Ad1-3 absent.

Ad4 with lateral and medial sections. Dorsally, both sections on posterior surface of Eb4; medial section beginning lateral to OP and continuing laterally about half distance to end of Eb4, dorsoposteromedially continuous with CT joining LE4 and LP (posterior Ad4 fibers separate from anterior fibers, which attach to Eb4 directly); lateral section on posterolateral portion of Eb4; ventrally both sections join Cb4 dorsally.

Ad5 dorsally relatively narrowly on Cb4 postero-lateralmost bony surface, ventrally relatively narrowly on Cb5 dorsolaterally.

SOD present.

RDs separated by distance less than diameter of one RD; extend ventrally, vertically from origins, producing excavation of SO in region of anteriorly extending SO longitudinal fibers, then turning anteriorly and attaching to medial edge of UP4 anteriorly, and continuing onto most of medial surface of Pb3 just dorsal to tooth plate.

Additional remarks. SCL attached mid-dorsally to tip of posteroventrally extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC absent. Eb4 levator process absent. Small AC present between Eb3 and Eb4 uncinat processes on right side. Pb1 bony with cartilaginous ends. Pb2 toothed.

BRAMIDAE

Brama brama, USNM 240541, 82.2 mm.

Plate 128

Description.

LE1 on raised bony dorsoposterior edge of Eb1 lateral to tip of uncinat process.

LE2 on raised bony dorsoposterior edge of Eb2.

LE3 absent.

LE4 on cartilaginous tip of Eb4 levator process; ventroposteriorly tendinous, continuous with broad CT sheet, which includes PP, that attaches along arches 4 and 5 and ventral edge of Ad5.

LP fine, fuses with anterolateral edge of LE4 insertion.

LI1 on Pb2 dorsoanterolaterally, extending slightly onto IAC at joint with Pb2.

LI2 on Pb3 posterolaterally anterior to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb4. TPb2 concave, roundish, with raised lateral edges, attaching ventroanteriorly to CT of pharyngeal roof, with mid-longitudinal raphe giving rise to CT sheets covering muscle; raphe mid-laterally with CT extension attaching to dorsoanterior cartilaginous edge of Pb2; free ventrolaterally from, but broadly continuous ventrally with, TEb2. TEb2 attaching on Eb2 dorsally anterior to LE2 insertion. TPb3-Eb4 acutely triangular, with apex becoming tendinous anteriorly and joining TPb2-TEb2 mid-ventroposteriorly, mainly attaching broadly on Eb4 bony surface dorsally medial to uncinate process with few fibers delaminating from ventral surface and inserting on Pb3 dorsoposteromedially; mid-posteroventrally continuous with SOD, which it overlaps dorsally and partially obscures in dorsal view.

OD3-4 origin broadly on Pb3 dorsally, insertion on Eb3 uncinate process anteriorly (and, on one side, on Eb3 dorsally just ventromedial to uncinate process) and medial edge of Eb4 uncinate process.

OP dorsally on Eb4 posteriorly beginning on levator process extending medially to uncinate process, there joining raphe with OD3-4 on one side but not other, laterally overlapping Ad4, which extends short distance medially anterior to OP; ventrally becoming tendinous and fascia-like and closely applied to posteromedial surface of Ad5; medially separable from SO, although fibers of both are closely adjacent.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteriorly beginning on levator process anteromedial to lateralmost edge of OP and extending to distal end, ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally narrowly on posterodistalmost surface of Cb4 (at edge of Eb4-Cb4 joint), ventrally moderately broadly on dorsolateralmost surface of Cb5, posterior surface fused to tendinous fascia-like ventral extension of OP.

SOD thin, dorsally ventral to TEb3-Eb4.

RDs adjacent.

Additional remarks. SCL attached weakly, if at all, mid-dorsally to elongate, posteroventrally extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed.

TOXOTIDAE

Toxotes jaculatrix (Pallas), USNM 331444, 94.2 mm; 289931, 86.9 mm.

Not illustrated

Description.

LE1 on Eb1 dorsoposteriorly a little lateral to tip of uncinate process; ventral half of lateral edge of muscle tendinous.

LE2 on Eb2 dorsoposteriorly about one-third distance from medial end of Eb2 and posterior to lateral end of TEb2; anterior muscle surface tendinous near insertion.

LE3 on Eb3 beginning at medial edge of tip of uncinate process and extending medially a short distance; ventral one-fourth of muscle lateral edge tendinous.

LE4 on Eb4 medial to levator process, ventrolaterally meeting LP, posteroventrolaterally joining narrow raphe with OP dorsolaterally; lateral surface of ventral third of muscle edge tendinous.

Remarks. The fine raphe with OP would hardly seem to qualify as a specialized character state, LE4 joins OP, but it is present on both sides of both specimens and as such is here considered to be a "sling" (sensus Stiassny and Jensen, 1987).

LP largest levator, on Eb4 dorsally beginning at lateralmost bony edge and extending medially, meeting LE4 insertion medially and cupping LE4 ventrally; LP insertion includes dorsal edge of Eb4 levator process, there meeting and joining raphe with muscular portion of PP, which continues ventrally as CT and all but encapsulates Ad5.

LI1 narrowly, tendinously on Pb2 dorsoanterolaterally; tendon continuous with CT binding anterior ends of Pb2 and Pb3 (see also description of TPb2); about same size as LI2.

LI2 on Pb3 dorsolaterally, meeting anterolateral end of TPb3-Pb4-Eb3 on Pb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 almost entirely anterior to TEb2, posteriorly overlapping a little of anterior edge of TEb2; muscle comprising an oval-shaped section on each side, which is angled a little anterolaterally from short mid-line raphe that widens and fills notch between ovals anteriorly and is continuous anteriorly with CT of pharyngeal roof; raphe continues posteriorly and becomes wide area of CT replacing central portion of TEb2 (leaving flat, dorsal Pb3 surfaces naked of muscle) and giving rise dorsally to CT sheets covering TD and attaching mid-ventrally to CT of pharyngeal roof. Anteroventrally, TPb2 attaches to joined dorsoanterior ends of Pb2 and Pb3 and dorsomedialmost surface of IAC, and is attached to anterior edge of ventral tendinous portion of LI1. TEb2 extends laterally and attaches on Eb2 dorsally anterior to LE2 insertion, muscle is dorsal to, and discontinuous with, TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 begins anteriorly on Pb3 dorsoposterolaterally at medial margin of LI2 insertion and continues posteriorly attaching onto posteromedial edge of Eb3, with strands extending from muscle ventral surface and attaching to Pb4 dorsally, continuous posteriorly by fine, diagonally crossing muscle strands with SOD anteriorly.

OD3–4 origin on Pb3 dorsomedially, insertion on Eb3 anteriorly beginning at tip of uncinat process and on medial edge of Eb4 beginning at tip of uncinat process, joining raphe with dorsomedial edge of OP on Eb4.

OP dorsally on Eb4 posteriorly beginning just ventral to tip of uncinat process, there meeting OD3–4, and extending laterally to just below tip of levator process, joining raphe dorsally with LE4, overlapping most to almost all of Ad4 dorsally; narrowly, ventrally on Cb5 posteriorly near distal end, muscle ventroposteriorly tendinous, joining raphe with Ad5 posteromedially.

Ad1–3 absent.

Ad4 broadly, dorsally on Eb4 ventrally beginning just anterior to medial end of OP and extending laterally to posterodistalmost bony surface; broadly, ventrally on Eb4 dorsally beginning about one third from medial end of bone and extending laterally to distal end of bone at inner corner of Eb4–Cb4 joint, posterolaterally meeting Ad5 on Eb4.

Ad5 dorsoanteriorly on Cb4 posterolaterally, posteroventrally on Cb5 dorsolaterally, anterior and posterior surfaces almost encapsulated by CT extending ventrally from PP.

SOD present.

Remarks. Johnson (1993:9) reported that *Toxotes* lacks SOD, but did not indicate the material on which he based his observations. He based it, however, on a set of gill arches that are from the same lot (USNM 289931) as one of the specimens on which the present description is based. If so, the muscles are damaged in the area where SOD would be expected and it is not possible to decide whether SOD might have been present. Johnson (1993:9) also reported SOD absent in *Scorpius*, *Kuhlia*, *Kyphosus*, and *Pholidichthys*, but, similarly, did not cite his material. Johnson based his observations on the following dissections: USNM 218922 (*Scorpius*), 289925 (*Kuhlia*), and 366512 (*Kyphosus*), all of which are damaged in the area where SOD might be expected to occur. Of these genera, and based on specimens dissected for the present study, we have found SOD lacking only in *Pholidichthys*. Our observations on these three genera are based on the following specimens: *Scorpius* sp. (USNM 339348) and *Kyphosus* (USNM 366512), both not otherwise discussed in the present study, and specimens cited in the description of *Kuhlia* (Kuhliidae).

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to tip of ventrally extending cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb1 bony with cartilage ends. Pb4 and UP4 present. Very reduced Eb4 flange present.

PLESIOPIDAE

Assessor macneilli Whitley, USNM 269466, 47.7 mm; USNM 274581, 51.7 mm.

Plate 129

Additional material. ② = *Paraplesiops poweri* Ogilby, USNM 274579, 92.2 mm. ③ = *Acanthoclinus fuscus* Jenyns, USNM 339246, not measured.

Description (based on smaller specimen of *Assessor* with remarks based on larger specimen).

LE1 on dorsoposterior rim of Eb1 beginning on uncinat process ventroanterolaterally and extending a short distance laterally.

LE2 on dorsalmost edge of raised, bony dorsoposterior rim of Eb2, well lateral to TEb2 insertion. ② Inserts posterior to distal end of TEb2.

LE3 on Eb3 immediately ventroanterior to cartilage tip of uncinat process.

LE4 finely, tendinously on Eb4 dorsally a little medial to dorsodistalmost end of bone, there meeting LP insertion (in smaller specimen, muscle inserts above levator process, which is absent in larger specimen). ② ③ Muscle massive, inserts broadly on Eb4 dorsally beginning laterally just anterior to levator process in ③ (process absent in ②), meeting OD3–4 posterodistally on Eb4; fusing with LP ventroanteriorly (or ventromedially, depending somewhat on viewing orientation) a little dorsal to insertion.

LP narrowly on dorsodistalmost end of Eb4 bony surface, meeting LE4 insertion ventroposteriorly. ② Muscle massive, ventroposteriorly joining raphe with Ad5 dorsally (thus, forming an unusual LP–Ad5 sling), fusing ventroanteriorly with LE4. ③ Massive like ②, but does not form LP–Ad5 sling.

LI1 larger than LI2, ventrally becoming moderately long, slender tendon passing ventral to TPb2 and inserting at junction between medial edge of Pb2 and adjacent impinging lateral edge of Pb3. ② ③ Muscularly and tendinously on Pb2 dorsoanteriorly posterior to anteriormost edge, tendinous portion continuing medially as strong, slender tendon inserting on Pb3 dorsal facet mid-dorsoanteriorly.

LI2 on Pb3 dorsoposterolaterally just medial to joint with Eb3; medial edge of insertion separated from lateral edge of TPb3–Eb3 in one specimen, meeting lateral edge of TPb3–Eb3 in other specimen. ② Medial edge meets lateral edge of TPb3–Eb3.

TD flat, comprises TPb2, TEb2, and TPb3–Eb3. TD with mid-longitudinal raphe, which gives rise dorsally to filmy CT sheets covering TD. TPb2 an anterolaterally extending muscle on each side, inserting on dorsoanterior surface of Pb2, almost completely anterior to TEb2. TEb2 dorsoanteromedially joining TPb2 ventrally; main anterior portion continuous dorsally from one side to the other ventral to TPb2, lesser posterior portion interrupted medially

LI2 on Pb3 posterolaterally anterior to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb4. TPb2 concave, roundish, with raised lateral edges, attaching ventroanteriorly to CT of pharyngeal roof, with mid-longitudinal raphe giving rise to CT sheets covering muscle; raphe mid-laterally with CT extension attaching to dorsoanterior cartilaginous edge of Pb2; free ventrolaterally from, but broadly continuous ventrally with, TEb2. TEb2 attaching on Eb2 dorsally anterior to LE2 insertion. TPb3-Eb4 acutely triangular, with apex becoming tendinous anteriorly and joining TPb2-TEb2 mid-ventroposteriorly, mainly attaching broadly on Eb4 bony surface dorsally medial to uncinata process with few fibers delaminating from ventral surface and inserting on Pb3 dorsoposteromedially; mid-posteroventrally continuous with SOD, which it overlaps dorsally and partially obscures in dorsal view.

OD3-4 origin broadly on Pb3 dorsally, insertion on Eb3 uncinata process anteriorly (and, on one side, on Eb3 dorsally just ventromedial to uncinata process) and medial edge of Eb4 uncinata process.

OP dorsally on Eb4 posteriorly beginning on levator process extending medially to uncinata process, there joining raphe with OD3-4 on one side but not other, laterally overlapping Ad4, which extends short distance medially anterior to OP; ventrally becoming tendinous and fascia-like and closely applied to posteromedial surface of Ad5; medially separable from SO, although fibers of both are closely adjacent.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteriorly beginning on levator process anteromedial to lateralmost edge of OP and extending to distal end, ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally narrowly on posterodistalmost surface of Cb4 (at edge of Eb4-Cb4 joint), ventrally moderately broadly on dorsolateralmost surface of Cb5, posterior surface fused to tendinous fascia-like ventral extension of OP.

SOD thin, dorsally ventral to TEb3-Eb4.

RDs adjacent.

Additional remarks. SCL attached weakly, if at all, mid-dorsally to elongate, posteroventrally extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed.

TOXOTIDAE

Toxotes jaculatrix (Pallas), USNM 331444, 94.2 mm; 289931, 86.9 mm.

Not illustrated

Description.

LE1 on Eb1 dorsoposteriorly a little lateral to tip of uncinata process; ventral half of lateral edge of muscle tendinous.

LE2 on Eb2 dorsoposteriorly about one-third distance from medial end of Eb2 and posterior to lateral end of TEb2; anterior muscle surface tendinous near insertion.

LE3 on Eb3 beginning at medial edge of tip of uncinata process and extending medially a short distance; ventral one-fourth of muscle lateral edge tendinous.

LE4 on Eb4 medial to levator process, ventrolaterally meeting LP, posteroventrolaterally joining narrow raphe with OP dorsolaterally; lateral surface of ventral third of muscle edge tendinous.

Remarks. The fine raphe with OP would hardly seem to qualify as a specialized character state, LE4 joins OP, but it is present on both sides of both specimens and as such is here considered to be a "sling" (sensus Stiassny and Jensen, 1987).

LP largest levator, on Eb4 dorsally beginning at lateralmost bony edge and extending medially, meeting LE4 insertion medially and cupping LE4 ventrally; LP insertion includes dorsal edge of Eb4 levator process, there meeting and joining raphe with muscular portion of PP, which continues ventrally as CT and all but encapsulates Ad5.

LI1 narrowly, tendinously on Pb2 dorsoanterolaterally; tendon continuous with CT binding anterior ends of Pb2 and Pb3 (see also description of TPb2); about same size as LI2.

LI2 on Pb3 dorsolaterally, meeting anterolateral end of TPb3-Pb4-Eb3 on Pb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 almost entirely anterior to TEb2, posteriorly overlapping a little of anterior edge of TEb2; muscle comprising an oval-shaped section on each side, which is angled a little anterolaterally from short mid-line raphe that widens and fills notch between ovals anteriorly and is continuous anteriorly with CT of pharyngeal roof; raphe continues posteriorly and becomes wide area of CT replacing central portion of TEb2 (leaving flat, dorsal Pb3 surfaces naked of muscle) and giving rise dorsally to CT sheets covering TD and attaching mid-ventrally to CT of pharyngeal roof. Anteroventrally, TPb2 attaches to joined dorsoanterior ends of Pb2 and Pb3 and dorsomedialmost surface of IAC, and is attached to anterior edge of ventral tendinous portion of LI1. TEb2 extends laterally and attaches on Eb2 dorsally anterior to LE2 insertion, muscle is dorsal to, and discontinuous with, TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 begins anteriorly on Pb3 dorsoposterolaterally at medial margin of LI2 insertion and continues posteriorly attaching onto posteromedial edge of Eb3, with strands extending from muscle ventral surface and attaching to Pb4 dorsally, continuous posteriorly by fine, diagonally crossing muscle strands with SOD anteriorly.

OD3–4 origin on Pb3 dorsomedially, insertion on Eb3 anteriorly beginning at tip of uncinat process and on medial edge of Eb4 beginning at tip of uncinat process, joining raphe with dorsomedial edge of OP on Eb4.

OP dorsally on Eb4 posteriorly beginning just ventral to tip of uncinat process, there meeting OD3–4, and extending laterally to just below tip of levator process, joining raphe dorsally with LE4, overlapping most to almost all of Ad4 dorsally; narrowly, ventrally on Cb5 posteriorly near distal end, muscle ventroposteriorly tendinous, joining raphe with Ad5 posteromedially.

Ad1–3 absent.

Ad4 broadly, dorsally on Eb4 ventrally beginning just anterior to medial end of OP and extending laterally to posterodistalmost bony surface; broadly, ventrally on Eb4 dorsally beginning about one third from medial end of bone and extending laterally to distal end of bone at inner corner of Eb4–Cb4 joint, posterolaterally meeting Ad5 on Eb4.

Ad5 dorsoanteriorly on Cb4 posterolaterally, posteroventrally on Cb5 dorsolaterally, anterior and posterior surfaces almost encapsulated by CT extending ventrally from PP.

SOD present.

Remarks. Johnson (1993:9) reported that *Toxotes* lacks SOD, but did not indicate the material on which he based his observations. He based it, however, on a set of gill arches that are from the same lot (USNM 289931) as one of the specimens on which the present description is based. If so, the muscles are damaged in the area where SOD would be expected and it is not possible to decide whether SOD might have been present. Johnson (1993:9) also reported SOD absent in *Scorpius*, *Kuhlia*, *Kyphosus*, and *Pholidichthys*, but, similarly, did not cite his material. Johnson based his observations on the following dissections: USNM 218922 (*Scorpius*), 289925 (*Kuhlia*), and 366512 (*Kyphosus*), all of which are damaged in the area where SOD might be expected to occur. Of these genera, and based on specimens dissected for the present study, we have found SOD lacking only in *Pholidichthys*. Our observations on these three genera are based on the following specimens: *Scorpius* sp. (USNM 339348) and *Kyphosus* (USNM 366512), both not otherwise discussed in the present study, and specimens cited in the description of *Kuhlia* (Kuhliidae).

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to tip of ventrally extending cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb1 bony with cartilage ends. Pb4 and UP4 present. Very reduced Eb4 flange present.

PLESIOPIDAE

Assessor macneilli Whitley, USNM 269466, 47.7 mm; USNM 274581, 51.7 mm.

Plate 129

Additional material. ② = *Paraplesiops poweri* Ogilby, USNM 274579, 92.2 mm. ③ = *Acanthoclinus fuscus* Jenyns, USNM 339246, not measured.

Description (based on smaller specimen of *Assessor* with remarks based on larger specimen).

LE1 on dorsoposterior rim of Eb1 beginning on uncinat process ventroanterolaterally and extending a short distance laterally.

LE2 on dorsalmost edge of raised, bony dorsoposterior rim of Eb2, well lateral to TEb2 insertion. ② Inserts posterior to distal end of TEb2.

LE3 on Eb3 immediately ventroanterior to cartilage tip of uncinat process.

LE4 finely, tendinously on Eb4 dorsally a little medial to dorsodistalmost end of bone, there meeting LP insertion (in smaller specimen, muscle inserts above levator process, which is absent in larger specimen). ② ③ Muscle massive, inserts broadly on Eb4 dorsally beginning laterally just anterior to levator process in ③ (process absent in ②), meeting OD3–4 posterodistally on Eb4; fusing with LP ventroanteriorly (or ventromedially, depending somewhat on viewing orientation) a little dorsal to insertion.

LP narrowly on dorsodistalmost end of Eb4 bony surface, meeting LE4 insertion ventroposteriorly. ② Muscle massive, ventroposteriorly joining raphe with Ad5 dorsally (thus, forming an unusual LP–Ad5 sling), fusing ventroanteriorly with LE4. ③ Massive like ②, but does not form LP–Ad5 sling.

LI1 larger than LI2, ventrally becoming moderately long, slender tendon passing ventral to TPb2 and inserting at junction between medial edge of Pb2 and adjacent impinging lateral edge of Pb3. ② ③ Muscularly and tendinously on Pb2 dorsoanteriorly posterior to anteriormost edge, tendinous portion continuing medially as strong, slender tendon inserting on Pb3 dorsal facet mid-dorsoanteriorly.

LI2 on Pb3 dorsoposterolaterally just medial to joint with Eb3; medial edge of insertion separated from lateral edge of TPb3–Eb3 in one specimen, meeting lateral edge of TPb3–Eb3 in other specimen. ② Medial edge meets lateral edge of TPb3–Eb3.

TD flat, comprises TPb2, TEb2, and TPb3–Eb3. TD with mid-longitudinal raphe, which gives rise dorsally to filmy CT sheets covering TD. TPb2 an anterolaterally extending muscle on each side, inserting on dorsoanterior surface of Pb2, almost completely anterior to TEb2. TEb2 dorsoanteromedially joining TPb2 ventrally; main anterior portion continuous dorsally from one side to the other ventral to TPb2, lesser posterior portion interrupted medially

and joining lateral margin of small, roundish CT pad overlying naked, flat Pb3 facet posteriorly; muscle extends laterally, attaching to Eb2 dorsally medial to LE2 insertion; muscle slip (absent in larger specimen) arises from TEb2 mid-anteriorly on right side and extends medially as fine tendon, which inserts on Pb2 near LI1 insertion. TPb3-Eb3 mid-antromedially continuous by CT with TEb2, attaches to Pb3 dorsoposteriorly along LI2 insertion and has fine CT attachment to anteromedialmost edge of Eb3; muscle continuous posteriorly by fine, diagonal muscle strands with SOD.

Remarks. The flat Pb3 dorsal facet forms the dorsomedialmost surface of Pb3. In the larger specimen of *Assessor*, TEb2 is continuous only by CT across the facets, the anterior one-third of each facet is ventral to TPb2; the posterior two-thirds are naked muscously. In the smaller specimen, only a small area of the facet is naked.

② Mid-dorsal CT area giving rise dorsally to tough CT sheets; most of Pb3 dorsal surface not covered by muscle; muscle fibers of anterior portion of TPb2 more-or-less transversely oriented, those of posterolateral portion thinner, more longitudinally oriented, two portions meet at fine CT notch laterally near point where ventroanterior edge of LI1 impinges on TPb2. TEb2 extends laterally to point anterior to LE2 insertion.

③ TPb2 and TEb2 muscously continuous across Pb3s; TEb2 like *Assessor*.

OD3-4 origin on Pb3 along and ventral to lateral edge of flat, dorsal Pb3 facet (ventral to roundish CT pad), insertion on Eb3 uncinat process dorsoanteriorly and Eb4 uncinat process medially. ② ③ Muscle massive.

OP in two parts, medial part dorsally on Eb4 posteriorly beginning just ventral to uncinat process and extending short distance laterally, posteriorly overlapping medial edge of lateral OP part, which extends laterally on Eb4 to below medial edge of LE4-LP insertions; ventrally two parts join raphe with ventroposterior surface of Ad5 dorsal to attachment to Cb5, and attach to dorsal surface of small, posterodistally projecting bony Cb5 process that extends laterally past medial margin of cartilage tip. OP of larger specimen comprises single part occupying same area as two parts of smaller specimen. ② Lateral portion much thicker than medial portion, overlying medial portion posteriorly. ③ Comprises single part.

Ad1-3 absent; fine GFM present. ② GFMs moderately well developed, that on arch 2 extending dorsally on Eb2 and just meeting distal end of TEb2.

Ad4 relatively small, dorsally on Eb4 ventroposteriorly lateral to lateral edge of OP, ventrally, narrowly on Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally moderately narrowly on Cb4 posterolaterally; ventrally very narrowly on Cb5 dorso-

distally. ② Very well developed, joining raphe dorsally with LP. ③ Like *Assessor*.

SOD relatively fine.

RDs narrowly separate.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 absent, UP4 present. Pb1 mostly bony. Pb2 toothed. IAC present.

Although, TV4 is free from Cb5s in *Paraplesiops*, it consists of two layers, dorsal and ventral. The ventral layer is muscously continuous and unmodified as it passes across the Cb5s, whereas, the dorsal layer changes to thick CT as it crosses the flattened ventroanterior tips of the Cb5s. Bony Eb4 flange present. Medial end of Eb4 smaller than that of Eb3, also true of *Trachinops* (USNM 269557), *Plesiops* (USNM 264268), and *Acanthoclinus* (USNM 200546), all cleared and stained specimens, and ③, but medial end of Eb4 is larger than medial end of Eb3 in *Paraplesiops*.

Mooi (1993:291) hypothesized the phylogeny of the Plesiopidae. He recognized *Trachinops* as comprising the basalmost clade of the family, *Assessor* as comprising the next clade, and *Paraplesiops* and *Acanthoclinus*, separately, as members of the next, and final two, clades. We, therefore, consider that the state of the medial end of Eb4 in *Paraplesiops* is apomorphic for that genus, as is the position of the lateral end of TEb2 reaching laterally anterior to LE2 insertion, which is usually unspecialized for perciforms. On the other hand, the muscously uninterrupted condition of TPb2 and TEb2 of *Acanthoclinus*, which generally appears to be plesiomorphic in perciforms, is apomorphic for *Acanthoclinus*.

PERCIDAE

Perca flavescens (Mitchill), USNM 193135, 91.7 mm.

Plate 130

Additional material. ② = *Percina caprodes* (Rafinesque), USNM 230758, 2:101-103 mm. ③ = *Percina sciera* (Swain), USNM 161594, 91.5 mm.

Description.

LE1 on Eb1 uncinat process just lateral to cartilage tip. ② ③ Uncinat process appears to have moved medially and fused with cartilaginous medial end of Eb1; anterior arm of Eb1 represented by slight cartilaginous bulge of ventromedial end in ②, which does not join Pb2; bulge absent in ③; muscle inserts on raised bony process on Eb1 mid-dorsoposteriorly.

LE2 on bony dorsoposterior surface of Eb2.

LE3 on cartilaginous tip of Eb3 uncinat process.

LE4 dorsoposteriorly on Eb4 just lateral to uncinat process.

LP on Eb4 at and lateral to LE4 insertion.

LI1 mainly on Pb2 dorsoanteriorly, but few muscle strands appear to continue into CT covering Pb2 and anterior end of closely joined Pb3. ② ③ Mainly on Pb2, but some muscle strands clearly continue onto Pb3.

LI2 on Pb3 dorsoposteriorly.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 thin, flat, laterally curving ribbon of muscle on each side arising from TEb2 at anterior end of mid-longitudinal raphe and continuing to posterior end of raphe; not attached to Pb2. TEb2 with mid-anterior and mid-posterior notches joined by mid-longitudinal raphe giving rise dorsally to sheets of CT and connecting ventrally to CT of pharyngeal roof; anterolateral and posterolateral converging fibers fusing before attaching on most of dorsal surface of Eb2. TPb3-Pb4-Eb3 on Pb3 dorsally just medial to LI2 insertion, extending onto dorsomedial end of Eb3 and, weakly, onto dorsal surface of Pb4, posteriorly continuous by diagonal slip of muscle with SOD. ② TPb2 thin, flat, laterally curving ribbon of muscle on only one side of each of two specimens. ② ③ TEb2 scarcely notched posteriorly; TPb3-Pb4-Eb3 on Pb3 dorsoposteriorly, Pb4 dorsally, and Eb3 dorsoposteromedialmost end.

OD3–4 origin broadly on Pb2 posterior to LI1 insertion and continuing broadly medially onto Pb3 ventral to TEb2, inserts on anterior surface of Eb3 uncinat process and anterior surface and medial edge of Eb4 uncinat process.

OP dorsally on all of bony posterior surface of Eb4 medial to LE4 insertion, ventrally on Cb5 bony surface beginning medial to distal end, overlapping posteriorly much of Ad5 posterior surface and joining Ad5 attachment to Cb5.

M. Pb2-Eb2 absent. ② On one side of one specimen, small strip of muscle extends from lateral edge of Pb2 to anterior edge of Eb2 anteroventral to TEb2. ③ On both sides, relatively broad strap of muscle originates on lateral edge of Pb2 ventral to OD3–4 and attaches to anterior edge of Eb2 ventral to TEb2.

Ad1–3 absent. ② ③ Ad1 on dorsoanterior surfaces of, and covering joint between, Eb1 and Cb1; Ad2 beginning medially at raphe with lateral end of TEb2, extending laterally and spreading anterolaterally and attaching to anterior surfaces of Eb2-Cb2 at joint; Ad3 broad dorsomedially, on dorsolateral surface of Eb3, spreading anterolaterally and attaching to anterior surfaces of Eb3-Cb3 joint.

Remarks. GFM (not illustrated) present in *Perca* in positions similar to Ad1–3, which attach to GFMs in ② and ③, but relatively weakly developed, hence, difference in interpretation.

Ad4 broadly dorsally on posterior surface of Eb4 lateral to OP; ventrally, less broadly on Cb4 dorsal surface anterior to Eb4-Cb4 joint, joining Ad5 attachment on Eb4.

Ad5 on Cb4 posterolateral surface and Cb5 dorso-posterior surface beginning lateral to OP attachment and extending medially anterior to OP attachment.

SOD present.

RDs slightly separated.

Additional remarks. SCL attached mid-dorsally to tip of cartilaginous ventroposterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC well developed. LE4 levator process absent. ② ③ Pb1 absent. ② IAC a tiny sphere on both sides in larger specimen, absent in smaller specimen. ③ IAC absent.

CEPOLIDAE

Cepola rubescens Linnaeus, USNM 285452, ca. 260 mm.

Plate 131

Additional material. ② = *Acanthocephala limbata* (Valenciennes), NSMT P. 64733, 375 mm.

Description.

Remarks. All levators and RDs relatively slender.

LE1 origin by short, fine tendon; insertion on dorsoanterior surface of Eb1 just ventral to cartilage tipped process lateral to uncinat process, which articulates with IAC; dorsoanterior surface of LE1, and entire anterior surface of Pb1, attaches to posterior surface of CT arising from anterior edge of Eb1.

LE2 on dorsoposteriormost edge of Eb2 posterior to lateral end of TEb2.

LE3 on tip of Eb3 uncinat process.

LE4 on bony surface of Eb4 immediately medial to cartilage tip of levator process, posteriorly joining LP insertion. ② On levator process together with LP.

LP beginning on tip of levator process and extending medially, joining LE4 insertion posteriorly. ② On levator process with LE4.

LI1 divides into anterior and posterior branches as it passes over Pb2 articulation with IAC, anterior branch inserts on dorsalmost surface of Pb2, posterior branch, inserts on Pb2 dorsally well ventral to anterior branch and continues onto adjacent lateral edge of Pb3 anterior process. ② IAC absent on both sides; insertion divided on only one side; insertion on other side passes posterior to Eb2-Pb2 joint and inserts like posterior branch of other side.

LI2 on Pb3 dorsoposterolaterally immediately medial to medial end of Eb3 anteriorly.

TD comprises TEb2, M. TEb2-Pb2, and TPb3-Eb3. TEb2 with mid-longitudinal raphe giving rise to CT pad dorsally and attaching anteriorly to CT of pharyngeal roof and laterally on Eb2 dorsally anterior to LE2 insertion; muscle is joined ventromedially by M. TEb2-Pb2, and is continuous mid-posteroventrally by fine, diagonal muscle strap with TPb3-Eb3 dor-

soanteriorly (② TEb2 not continuous with TPb3-Eb3). M. TEb2-Pb2 broad, strap-like, originating ventrally from TEb2 posteriorly and extending anteriorly along mid-longitudinal raphe for about half length of raphe (② muscle originates along mid-posterior half of raphe); muscle extends ventroanterolaterally dorsal to OD3–4 origin and inserts on Pb2 dorsomedially just posterior to base of dorsoanterior process. TPb3-Eb3 on Pb3 dorsally beginning anterior to joint with medial end of Eb3 and extending posteriorly and attaching to posteromedial corner of Eb3 on both sides, but on one side a fine, probably anomalous, muscle strand extends to opposite side and attaches to anteromedial edge of Eb4. (② No attachment to Eb4); muscle continuous posteriorly with SOD. ② TPb3-Eb3 joins raphe posterolaterally on each side with SO muscle strap passing dorsoanteriorly immediately lateral to OP on Eb4.

Remarks. M. TEb2-Pb2 is not present in any other acanthomorph we examined. It is difficult to equate the muscle with TPb2, which arises dorsal and/or anterior to TEb2. If present in *Owstonia* and/or *Sphenanthias*, M. TEb2-Pb2 will either represent another synapomorphy of the Cepolidae or it will define a monophyletic group within the family.

OD3–4 origin of Pb3 dorsally ventral to M.TEb2-Pb2, beginning a little posterior to anteriormost tip of Pb3; insertion on Eb3 anteriorly just ventral to tip of uncinat process and on bony medial edge of Eb4 uncinat process.

OP strap-like; dorsally on Eb4 posteriorly beginning medially ventral to tip of uncinat process and extending laterally about half distance between uncinat and levator processes (② extends to or almost to levator process); ventrally on Cb5 beginning laterally on distal cartilaginous end medial to Ad5, and extending medially a short distance and meeting TV5.

Ad1–3 absent. GFM1–3 moderately developed.

Ad4 on Eb4 dorsoposteriorly beginning medially just medial to lateral edge of OP and extending laterally to distalmost bony edge, ventrally on Cb4 dorsally beginning at Eb4-Cb4 joint and extending medially a short distance.

Ad5 short, ventrally on Cb5 posterodistally, dorsally on Cb4 posterodistally and AC4 posteriorly. ② does not join AC4.

SOD slender.

RDs separated by distance greater than diameter of one RD. ② Separated by about one-half RD diameter.

Additional remarks. SCL attached mid-dorsally to ventrally extending posterior cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. ② SCL attached mid-posteriorly to ventroanteriormost surface of ventrally extending posterior cartilaginous tip of Bb3. IAC small, ball-like; AC4 relatively small. ② IAC absent; AC4 relatively large.

The presence of two uncinat processes on Eb1 is unique among the Actinopterygii (the tip of the lateralmost process is attached by CT to Eb2 anteriorly). Gill and Mooi (1993:331 and fig. 2) noted that two rod-like uncinat processes on Eb1 support monophyly of the Cepolidae and Owstoniidae, which they recognized, as do we, as a single family, Cepolidae. Nelson (1994:378), however, recognized both families in a superfamily Cepoloidea.

CALLANTHIIDAE

Callanthias allporti Günther, USNM 350940, 129 mm.

Plate 132

Additional material. *Callanthias australis* Ogilby, AMS I.18079–002, 87.9 mm. ② = *Grammatonotus laysanus* Gilbert, BPBM 22757, 126 mm.

Description.

Remarks. We noted no substantive differences in the musculature between the two species of *Callanthias*, or in the skeletal structure in both genera. Differences reported are for *Grammatonotus*.

LE1 on dorsal edge of Eb1 immediately lateral to broad uncinat process, continuing very slightly onto CT joining Eb1 and Eb2.

LE2 on posterodorsal edge of Eb2 a little lateral to mid-length and continuing on CT between Eb2 and Eb3; muscle is cleanly divisible into two sections, one on bone and one on CT.

LE3 on tip of Eb3 uncinat process.

LE4 on tip of Eb4 levator process.

LP on Eb4 levator process at and lateral to LE4 insertion.

LI1 on dorsal bony edge of Pb2 uncinat process just posterior to cartilaginous tip.

LI2 on Pb3 dorsolaterally at and anterior to medial end of Eb3.

TD comprises TEb2, and TPb3-Pb4-Eb3. Thick CT pad attaches anterolaterally to anteriormost end of Pb2 and mid-anterioventrally to anterior end of mid-longitudinal TEb2 raphe, which joins CT of pharyngeal roof. TEb2 attaches ventrally along mid-longitudinal raphe to CT of pharyngeal roof; muscle extends laterally attaching along most of Eb2 dorsal surface; TEb2 not continuous with TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 on Pb3 dorsal bony surface medial to medial end of Eb3, continuing posteriorly onto posteromedialmost edge of Eb3 and adjacent dorsomedial edge of Pb4, continuous posteriorly by diagonal muscle straps with SOD. ② Attachment to medial end of Eb3 absent, hence TPb3-Pb4.

OD3–4, OD3' origin on dorsoanterior surface of Pb3 ventral to TEb2, splitting shortly into dorsal (OD3) and ventral (OD4; not illustrated) sections.

Dorsal section completely overlies ventral section, hiding it in dorsal view; dorsal section splits laterally with ventroanterior portion (OD3') inserting on Eb3 dorsal surface well ventral to uncinat process and dorsal portion (OD3) inserting on anterior surface of uncinat process. Ventral section inserts on Eb4 anterior surface medial to levator process. ② OD3' absent; OD3–4 attachment on Eb4 only to tiny section of dorsal edge of Eb4 ventromedial to levator process (Eb4 section essentially absent).

Remarks. The Eb3 uncinat process is tightly joined to Eb4, which has lost the uncinat process. That the Eb4 process posterior to this joining is not a displaced uncinat process is evidenced by the insertions of LE4 and LP on the process. These two muscles rarely, if ever, insert on the Eb4 uncinat process.

OP broadly on posterior surface of Eb4 medial to base of levator process and broadly on posterodistal surface of Cb5 posterior to Ad5.

Ad1–3 moderately developed, but gill-filaments attach to these muscles and they could be interpreted simply as well-developed cord-like GFM, present on Ebs and extending only to dorsoanteriormost surface of respective Cbs; however, Ads1–3 well developed in ②.

Ad4 broadly on posterior surface of Eb4 beginning at levator process and extending laterally, ventrally on posterodorsal surface of Cb4 medial to Eb4-Cb4 joint.

Ad5 small, on posterodistal surface of Cb5, partly anterior to OP ventral attachment, and on distalmost cartilaginous tip of Cb4 posteriorly.

SOD present.

RDs well separated.

Additional remarks. SCL attached mid-dorsally to tip of ventrally extending posterior cartilaginous end of Bb3. TV4 free from Cb5s. Pb1 cartilaginous. Pb4 and UP4 present IAC present. Eb4 uncinat process absent. ② SCL questionably absent (should be verified in another specimen); Pb1 cartilaginous, very slender, embedded in tough CT; one side in two segments.

GERREIDAE

Gerres cinereus Eigenmann, USNM 331928, 90.4 mm; USNM 337861, 2: 60.9–95.7 mm.

Plate 133

Additional material. ② = *Eucinostomus* sp., USNM 342106, 92.7 mm.

Description.

LE1 tendinously and muscously on anterior surface of Eb1 uncinat process just ventral to cartilaginous tip.

LE2 narrowly tendinously and muscously on tip of bony process on Eb2.

LE3 tendinously and muscously on dorsomedial bony edge of Eb3 uncinat process.

LE4 tendinously on mid-dorsoposterior surface of Eb4, fusing with medial end of LP insertion. ② Insertion not fused with that of LP.

LP massive, on much of dorsoposterior edge of Eb4, fusing with LE4 insertion, meeting, but not joining OP dorsally. ② Smaller than LE4, insertion entirely lateral to that of LE4.

LI1 tendinously and muscously on bony posterior surface of Pb2 dorsoanterior process ventral to cartilaginous tip, with tendon continuing ventrally to posterior surface of dorsoanteriormost Pb3 process.

LI2 slender tendinously on Pb3 posterolaterally ventral to medial end of Eb3, which overlies Pb3.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 pair of muscles, each member joined to lateral edge of thick CT pad covering Pb3 dorsal articulating facets and attaching on medial half of Eb2 dorsal surface lateral to LE2 insertion. TPb3-Eb3-Eb4 on dorsoposterolateral surface of Pb3, posteromedialmost edge of Eb3, and dorsomedialmost surface of Eb4.

OD3–4, OD3'. OD3–4 origin on lateral edge of Pb3 dorsal articulating facet, insertion on medial edge and anterior surface of Eb3 uncinat process and medial edge and posterior surface of Eb4 uncinat process; just posterior to origin, OD3' originates with OD3–4, diverges well laterally and inserts on dorsal surface of Eb3 ventral to uncinat process, forming raphe with posteromedial end of Ad3; OD3' absent in 60.9 mm specimen and ②.

OP massive, on much of posterior surface of Eb4 and extending ventrally and attaching by tendons to posterior surface of Cb5 somewhat medial to distal end; Ad5 fibers joining OP tendons anteriorly; slender, separate OP strap attaches dorsally narrowly to Eb4 medial to massive OP attachment and to Cb5 medial to Ad5 attachment.

Ad1 relatively small, restricted, spans anterior surface of Eb1-Cb1 joint.

Ad2 begins on Eb2 dorsoanteriorly adjacent to lateral end of TEb2 and expands laterally attaching over anterior surface of Eb2-Cb2 joint.

Ad3 begins medially at raphe with lateral end of OD3' and expands laterally attaching over anterior surface of Eb3-Cb3 joint. In smallest and largest specimens and ② occupies most of dorsal and anterolateral surfaces of Eb3 (area of attachment equals that of OD3' + Ad3 of 90.4 mm specimen).

Ad4 on ventral surface of Eb4 and dorsal surface of Cb4 medial to Eb4-Cb4 joint; completely excluded from view posteriorly.

Ad5 dorsally tendinously on distal end of Cb4, tendon continues onto distal end of Eb4; muscle fusing

(larger specimen) or not anteriorly with OP, ventrally on Cb5 distal end.

SOD present.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to ventroposteriorly extending cartilaginous tip of Bb3. TV free from Cb5s. Rosen and Patterson (1990:13) reported that Pb4 is absent in gerreids. Although it is reduced in size, we find that it and UP4 are present. IAC present. Eb4 levator process absent. Well-developed bony flange (occluded from view by LP in Plate 133) at end of Eb4, completely overlies cartilaginous distal end of Eb4. Medial end of Eb4 varies in diameter from about equal to a little larger than that of Eb3, but is smaller than that of Eb3 in ② (two cleared and stained specimens of *Eucinostomus*, USNM 397354 and 306708, also examined for this character).

GRAMMATIDAE

Gramma loreto Poey, USNM 369710, 53.3 mm; 199487, 54.4 mm; 319222, 50.9 mm; 360710, 52 mm.

Plate 134

Description.

LE1 on dorsoposterior edge of Eb1 lateral to uncinat process.

LE2 on dorsoposterior surface of Eb2 at about mid-length.

LE3 on Eb3 uncinat process just ventral to cartilaginous tip.

LE4 on bony edge of Eb4 levator process just medial to cartilaginous tip.

LP on bony edge and cartilaginous tip of Eb4 levator process, joining LE4 insertion posteriorly.

LI1 broad; finely tendinously on anterolateralmost edge of Pb3 adjacent to medial edge of Pb2.

LI2 on Pb3 dorsoposteriorly along medial edge of attachment of TPb3-Pb4 and near medial end of Eb3.

TD comprises TEb2 and TPb3-Pb4. TEb2 a pair of muscles, each separated from (and continuous with) counterpart by CT band equal to width of area separating Pb3s; each element of pair comprising anterior and posterior portions, anterior portion attaches to dorsal surface of Eb2 anterior to LE2 insertion, posterior portion attaches to posterior surface and edge of Eb2 medial to LE2 insertion; free from TPb3-Pb4. TPb3-Pb4 on Pb3 dorsal surface medial to LI2 insertion and on anterior edge of Pb4, continuous posteriorly by diagonal strands of muscle with SOD.

OD3-4 origin on dorsal surface of Pb3 ventral to TEb2, insertion on dorsoanterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally on Eb4 posterior surface beginning

below LP and extending medially for variable distance (unclear separation from SO on one side), ventrally on Cb5 dorsodistally posterior to Ad5.

Ad1-3 absent.

Ad4 dorsally on Eb4 beginning below LP insertion and continuing laterally to near distal end of Eb4, ventrally on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 on dorsoposterior end of Cb5 anterior to OP and on posterior surface of Eb4-Cb4 joint.

SOD present.

RDs separate.

Additional remarks. SCL free from Bb3 (cartilaginous posterior end not elongate). TV4 ventrally continuous across Cb5s, but dorsally attaching to Cb5s (necessary to bisect muscle ventrally to expose attachment). Pb4 present. UP4 present. IAC present.

OPISTOGNATHIDAE

Lonchopisthus higmani Mead, USNM 186058, 73.1 mm; USNM 292182, 85.1 mm.

Plate 135

Additional material. ② = *Opistognathus darwiniensis* Macleay, USNM 174042, 60.5 mm.

Description.

LE1 on anteroventral surface of Eb1 uncinat process.

LE2 on dorsoposterior surface of Eb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 adjacent to tip of levator process anteriorly. ② Broadly on Eb4 dorsoposteriorly (levator process absent).

LP at and posterior to LE4 insertion.

LI1 on tendinous covering of anterior end of Pb2 dorsolaterally, covering continues medially over adjacent anterior end of Pb3.

Remarks. Articulation of Pb1 with anteromedial tip of Eb1 joins tiny CT pad that covers joined anterior ends of Pb2 and Pb3. Pb2 edentate. ② Condition of preparation prevented determining if tiny CT pad was present.

LI2 on Pb3 dorsoposterolaterally, lateral to attachment of TPb3-Eb3-Eb4 and just medial to joint with medial end of Eb3.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 a pair of muscles connected by tough CT across flat dorsal Pb3 surfaces, CT continuous anteriorly between Pb3s with CT of pharyngeal roof; muscle extending laterally on Eb2 dorsal surface anterior to LE2 insertion. TPb3-Eb3-Eb4 on Pb3 dorsoposteriorly well medial to LI2 insertion on right side and at medial edge of insertion on left side, with tendinous attachments (not illustrated) to medialmost ends of Eb3 and Eb4, continuous mid-posteriorly by crossing muscle strands with fine SOD. ② Thick CT pad over Pb3 dorsal surfaces; pad continuous with CT

joining TEb2 muscular portions, partially separable from more ventral CT covering and attaching directly to Pb3s.

OD3–4 origin ventral to TEb2 on posterolateral edge of Pb3 flat dorsal surface, insertion broadly on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process, cartilage tip of which is extremely small in smaller specimen and absent in larger specimen. ② On anterior surface of Eb3 uncinat process and dorsal edge of Eb4, which is attached to Eb3 uncinat process (no Eb4 uncinat process).

OP dorsally on posterior surface of Eb4 beginning at levator process and continuing well medial to uncinat process, ventrally broadly on Cb5 beginning laterally a little medial to distal end. ② Dorsally, broadly on posterior surface of lateral half of Eb4, posteriorly overlapping and almost completely excluding Ad4 from posterior view.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly beginning at levator process and extending laterally to just medial to distal end, ventrally on Cb4 dorsally medial to Eb4-Cb4 joint, fusing there with anterior surface of Ad5.

Ad5 dorsally on posterodistal end of Cb4, ventrally on Cb5 dorsodistally.

SOD present.

RDs slightly separated.

Additional remarks. SCL present. TV4 two layered, ventral layer free from Cb5s; dorsal layer divided mid-longitudinally, each portion attached to respective Cb5 lateral surface. IAC present ② Each dorsal portion attaches to ventral edge of respective Cb5. Pb4 and UP4 present.

PSEUDOCHROMIDAE

Labracinus cyclophthalmus (Müller and Troschel),
USNM 290900, 2 specimens, 78.3–82.4 mm;
USNM 345601, 90.7 mm SL.

Plate 136

Additional material. ② = *Pseudochromis porphyreus*
Lubbock and Goldman, USNM 290595. ③ =
Pseudochromis persicus Murray, USNM 147902.

Description.

Remarks. The muscles of both species of *Pseudochromis* are essentially the same as those of *Labracinus*.

LE1 on Eb1 posteriorly just lateral to base of uncinat process.

LE2 on raised posterior margin of Eb2.

LE3 on and lateral to Eb3 uncinat process anteriorly.

LE4 massive, on Eb4 dorsolateral surface.

LP narrowly on Eb4 dorsal surface at and posterior

to LE4 insertion, completely covering minute tip of levator process. ② Levator process very reduced on one side, absent on other. ③ Levator process like *Labracinus*.

LI1 tendinously on fascia covering anterior end of Pb2 (which overlaps Pb3) and continuing onto dorsolateralmost edge of Pb3.

LI2 on Pb3 dorsoposterolaterally just anterior to medial end of Eb3.

TD comprises TPb2a, TEb2, and TPb3-Eb3 (TPb3-Eb3-Eb4 in largest specimen). TPb2a on anterior surfaces of Pb2s, with mid-ventral raphe continuing posteriorly and joining thick CT pad covering most of dorsal surfaces of Pb3s, which are only partly roofed by muscle. TEb2 a pair of muscles joined medially by broad area of CT and joining mid-ventral surface of CT pad overlying Pb3 articulating facets; muscle extending laterally and attaching to Eb2 dorsoanteriorly unusually well lateral to LE2 insertion; TEb2 not continuous posteriorly with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsoposteriorly ventral and lateral to articulating facet and posteromedial end of Eb3 (and finely, tendinously on Eb4 dorsoanteromedially in largest specimen); continuous posteroventrally by diagonal muscle strand with SOD.

CPb originates posteriorly from longitudinal SO layer, extends anteriorly between Pbs, with continuous major branch extending anterolaterally around Pb2s and attaching to each UP4 anterolaterally; minor branch extends posteromedially from continuous major branch, passes medial to Pb3 and attaches to UP4 medially.

OD3–4 origin on Pb3 dorsoposteriorly ventral to TEb2, insertion broadly on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally on most of Eb4 posterior surface, ventrally broadly on Cb5 dorsoposteriorly.

Ad1 anterodistally on Eb1 and Cb1.

Ad2 medially joins raphe with distal end of TEb2 on anterior edge of Eb2 and extends laterally attaching on anterior surfaces of Eb2 and Cb2 at Eb2-Cb2 joint.

Ad3 medially on Eb3 dorsally ventral to lateral portion of OD3–4, laterally attaching to anterior surfaces of Eb3 and Cb3 at Eb3-Cb3 joint.

Ad4 broadly on Eb4 ventrally almost entirely anterior to OP, ventrally broadly on Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally on Eb4-Cb4 joint posteriorly, continuing, ventrally on Cb5 broadly anterodistally anterior to OP.

SOD slender.

RDs adjacent.

Additional remarks. SCL present. TV4 dorsal section attaches to Cb5s anteriorly, ventral section continuous across anteroventral ends of Cb5s. Pb4 and

UP4 present. Pb2 toothed. Eb4 levator process with minute cartilage tip.

Cb5 bears a tiny bit of cartilage at or near its distal end in *Labracinus*, but is usually completely ossified in *Pseudochromis*, although there is a "spot" of cartilage on one Cb5 laterally well anterior to its distal end in ③. *Labracinus* has a tiny IAC, which is absent in ② and ③. *Labracinus* has a tiny, cartilaginous Pb1. ② Pb1 has relatively long cartilaginous dorsal and ventral ends separated by small central ossified area. ③ Pb1 state unknown.

LEIOGNATHIDAE

(See additional remarks following description for discussion of valid family name for this taxon.)

Gazza sp., USNM 268914, 2 specimens, 68.6–69.2 mm.

Plate 137

Additional material. ② = *Leiognathus equula* Forsskal, USNM 349512, 58.6 mm. ③ = *Secutor insidiator* (Bloch), USNM 329585, 70.9 mm.

Description.

LE1 broadly on Eb1 dorsolaterally and on anterior and medial surfaces of large, dorsally expanded triangular process at lateral end of Eb1 (lateral surface of process concave, receives gill filament bases; process apparently not an uncinat process as similar process is serially present on Eb2 and gill filaments are not known to attach to Eb1 uncinat process; cartilaginously tipped uncinat process absent); muscle with lateral tendinous portion extending to origin. ② Like *Gazza*, but lateral edge of Eb1 not expanded nearly as much. ③ Narrowly, tendinously on Eb1 posterolaterally medial to scarcely expanded lateral end of Eb1.

LE2 on medial edge of large, dorsally expanded triangular process at lateral end of Eb2; ventrolaterally joining raphe with posterolateral edge of TEb2; gill filaments attach to concave lateral edge of triangular process. ② ③ Lateral end of Eb2 not expanded dorsally nearly as much as in *Gazza*.

LE3 muscously and, variably, tendinously on bony portion of Eb3 uncinat process anteriorly (process has minute cartilage tip posteromedially, visible only after separation from Eb4 uncinat process).

LE4 + LP fuse, well dorsal to Eb4, along tendinous raphe and form arms of a Y; raphe continues along anterior edge of muscular shank of Y, which is presumably formed by lateral section of OP, and attaches between uncinat process and lateral end of Eb4 posteriorly; another tendinous raphe extends along lateral section of OP posteriorly and attaches to hook-like cartilaginous distal end of Cb4; latter tendinous raphe on Cb4 expands into CT sheet that continues dorsoposteriorly as PP (not illustrated);

dorsoposteriorly, ventromedial portion of medial OP section attaches to Cb5 posterolaterally. ② Tendinous continuation from fused LE4 + LP continues along anterior edge of lateral OP section and attaches to posterodistalmost bony edge of Eb4, OP continues ventrally and meets Ad5 on Cb5; tendinous raphe absent along lateral section of OP posteriorly. ③ LE4 + LP fuse along strong tendon that divides before attaching between uncinat process and distal end of Eb4, tendon divides ventral to attachment, with lateral section of OP attaching to it.

LI1 on Pb2 anterolaterally well ventral to cartilage-tipped dorsally extending process of Pb2.

LI2 tendinously on Pb3 just medial to joint with posteromedial end of Eb3.

TD comprises TEb2 and TEb3-Eb4. TEb2 comprises a muscle on each side joined medially by tendinous CT to ventrolateral edge of a thick, cone-shaped CT pad (attenuated end ventral) that attaches medially to a conforming dorsal shelf of Pb3 and sits freely in a conforming depression of dorsoanterior surface of OD3–3'; pads on either side joined by CT dorsally across dorsal edge of conforming Pb3 shelf; TEb2 attaches on Eb2 dorsally, joining LE2 ventroanteriorly and extending well lateral to it; muscle free from TEb3-Eb4. TEb3-Eb4 on Eb3 posterior edge medial to base of uncinat process, continuing posteriorly and passing dorsal to medial end of Eb4 but attaching ventrally to posteromedial edge of Eb4 and, on left side only of one specimen, joining dorsomedial edge of OP medial section; muscle ventroanteriorly continuous by diagonal muscle strand (obscured from view in illustration) with SOD. ② ③ TD comprises TEb2 and TEb3; TEb3 attaches on medial edge of Eb3 uncinat process ventral to OD3 insertion.

OD3, OD3' massive, joint origin on lateral surface of conforming Pb3 dorsal shelf (see description of TEb2), dividing laterally with small OD3 section inserting on Eb3 uncinat process dorsoanteriorly, and large OD3' section inserting separately on remainder of Eb3 uncinat process anteriorly immediately ventral to OD3, insertion continues ventrally covering all of bony dorsolateral surface of Eb3 (superficially appears as if OD3 and OD3' are entirely fused; separation most distinct in ③).

OD4 absent.

OP presumably in two sections, for lateral section see LE4 above; medial section dorsally, broadly on Eb4 posterolaterally, ventrally more broadly on Cb5 posteriorly, joining posterior raphe of OP lateral section with Ad5 posteriorly; lateralmost portion of medial OP section joining tendinous raphe with lateral OP section on posterodistal end of Cb4 where raphe expands into CT sheet which continues to PP (not illustrated). ② Posterior raphe of lateral OP section

absent; two OP sections join on Cb5; CT of PP attaches to distal end of Cb5.

M. SO-Pb2 strap of SO longitudinal fibers extending anteriorly and inserting on Pb2 posteroventrally, passes posteriorly along Pb3 medially and then ventral to TEb3-Eb4 and, on left side only, divides, with one portion inserting on Eb4 at and medial to OP medial section and the other becoming continuous with SO and SOD anteriorly; on right side, Eb4 insertion is absent.

Remarks. This muscle does not insert on Eb4 in *Leiognathus* (only one side is adequate for determination) or on one side in *Secutor*, but does insert on Eb4 on the other side.

Ad1–3 absent.

Ad4 relatively small, scarcely if at all visible externally, on Eb4 ventrally and Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 small, on dorsodistal end of Cb5 and cartilaginous finger-like process at distal end of Cb4, joining short raphe there with ventromedial end of OP lateral section and ventrolateral end of OP medial section.

SOD slender.

RDs well separate anteriorly, swelling posteriorly and becoming proximate, each consisting of strap-like lateral section, RD', and much larger medial section, RD. RD' anteroventrally continuous (infiltrated?) with CT of SO and inserting on UP4 and Pb4 posteriorly; RD with minor insertion on posteromedial edge of UP4 and major insertion on Pb3 posteriorly.

Additional remarks. SCL weakly attached mid-anteriorly to posteroventrally extending cartilaginous end of Bb3 (SCL easily separated from Bb3). TV4 mostly continuous ventrally, but dorsoanterior fibers attach to anterolateral surfaces of Cb5s (hence similar to condition in to many other fishes that have an LE4-OP sling; e.g., labrids, cichlids, centrogenyids). Pb4 and UP4 present. IAC absent. Eb4 with small, bony flange dorsally at distal end. Dorsal end of Pb1 bony; . ② Dorsal end cartilaginous. Eb1 uncinat process absent. Eb3 uncinat process with minute cartilaginous tip. ② Cartilage tip of uncinat process normal. ③ Tip of process bony on both sides. Eb4 uncinat process present. ③ Uncinat process on one side with minute cartilage tip, bony tip on other side. Eb4 levator process absent in all.

Correct family name. Bleeker (1859:xxiii) coined the family name Equuloidei, in which he included fishes currently recognized in the families Leiognathidae and Menidae. Equuloidei was emended to Equulidae by Gill (1893:134), which Gill listed as a synonym of "Leiognathidae Gill, 1892." We were unable to find an 1892 or earlier publication of Gill's that refers to Liognathidae.

Equuloidei Bleeker was based on the genus *Equula* Cuvier, which is a junior synonym of *Leiognathus*

Lacepède; however, Equulidae has date seniority over Liognathidae Gill (first emended as Leiognathidae by Jordan and Evermann, 1902:338). Hence, Equulidae has seniority and, ostensibly, should replace Leiognathidae, but as far as we can tell has not been used as a senior synonym since before 1899. Leiognathidae has been used as a valid senior synonym for the family for many years and we elect to continue to use it and recommend that Equulidae be suppressed.

POLYCENTRIDAE

Remarks. Until recently (Britz, 1997), *Polycentrus*, *Polycentropsis*, *Monocirrhus* and *Afronandus* were included with *Nandus* in the family Nandidae. Britz (1997) demonstrated that a Nandidae that included these four genera was polyphyletic and removed them. He hypothesized the monophyly of the first three genera based on egg morphology, but only "tentatively" included *Afronandus* with them based on a single shared character: presence of adhesive filaments on the vegetal egg pole. Britz noted that this character also had been reported for some Pseudochromidae and Cichlidae, which he indicated were not closely related to the Nandidae, but he did not assign either the first three or all four genera to a separate family. Berra (2001:427), based on Britz (1997), apparently was first to define the Polycentridae as comprising only these four genera. Kullander and Britz (2002:301) similarly recognized a Polycentridae, but again only "tentatively" included *Afronandus*, based on Britz's (1997) character, which they erroneously described as "presence of attachment filaments around the micropylar area of the egg."

We find at least three synapomorphies, in addition to the vegetal-pole filaments, that support monophyly of the Polycentridae: loss of LE3, loss of sensory canals on most lateral-line scales (including all of those on posterior half of body), and presence of slender ligament attaching dorsal margin of Eb1 anterior to LE1 to ventral surface of skull at or near origin of LE1.

Notwithstanding its unilateral vestigial condition in *Monocirrhus* and *Afronandus*, loss of LE3 is a relatively uncommon character state for percomorphs (various scorpaenoids, Psettodidae, many smegmamorphae, Bramidae, Uranoscopidae, dactyloscopid blennioids, callionymids, gobiesocids). Absence of lateral-line scale tubes, or restriction of the tubes to a limited area on the anteriormost portion of the body, is also uncommon in perciform fishes, particularly those inhabiting freshwaters, although Britz (pers. comm.) informs us that the condition is also true of some deeply nested taxa within the Anabantoidae. Among freshwater percomorphs, the reduction or absence of tubed lateral-line scales is generally restricted to mugilids, various atherinomorphs and

gasterosteomorphs, elassomatids, percichthyids, nanoperoids, and specialized members of other groups (e.g., gobiids). The distribution of the Eb1 ligament in perciforms is less well known, as we may have overlooked or removed it in some taxa early in our study (see Introduction, methods section); however, it is not present in anabantoids, ambassids, and *Toxotes*. We have noted the ligament at least in pempherids, cirrhitids, bathyclupeids, lacteriids, acropomatids.

Another character, presence of a hook-like post-premaxillary process (reduced in *Afronandus*), is also uncommon among acanthomorphs, and may represent another polycentrid synapomorphy (see Liem, 1970:figs. 13–16). A similar post-premaxillary process is also present in *Nandus* (Liem, 1970:fig. 12), but is reduced in the closely related *Badis*, possibly a reflection of the small size attained by this genus.

Liem (1970), who examined the osteology and gill-arch musculature of all four polycentrid genera, included those genera in the Nandidae, along with *Nandus*, which he also examined (Liem, 1970:9, 11). Liem (1970:56) reported that all five genera had only three external levators, but did not indicate which levator was missing. He suggested that the posteriormost levator might represent a fusion of the third and fourth. Liem was correct in asserting that *Polycentrus*, *Polycentropsis*, *Monocirrhus* and *Afronandus* have only three LEs (he could easily have missed a vestigial LE3, if present, which we found unilaterally in *Afronandus* and *Polycentropsis*), but he was incorrect in implying the presence of only three LEs in *Nandus*, in which LE3 and LE4 are both well developed. Commonly in acanthomorphs, including *Nandus*, LE3 and LE4 appear to be fused along their entire length, except for their easily overlooked separate insertions on the surfaces of Eb3 and Eb4. LE3 and LE4 are easily separated and there is no intermingling of their fibers.

Other specializations shared by the polycentrids are the absence of SOD and Pb4 and the presence of more than three anal-fin spines and only one epural. All these characters have a broad and varied distribution.

In summary, the specializations shared by the four polycentrid genera, strongly imply their monophyly.

Polycentropsis abbreviata Boulenger, USNM 302514, 34.2 mm.

Not illustrated

Additional material. ② = *Polycentrus schomburgkii* Müller and Troschel, USNM 226071, 43.0 mm.

Description.

Remarks. The arrangements of the muscles, except for TD, are very similar in the two taxa.

LE1 on Eb1 posteriorly noticeably lateral to cartilage tip of uncinat process. Slender ligament originates on skull with LE1 and inserts on Eb1 anterior margin anterior to LE1 insertion.

LE2 on Eb2 about mid-dorsoposteriorly.

LE3 present only on left side; thread-like, less than 10% width of LE4, inserting on tip of Eb3 uncinat process. ② Absent on both sides.

LE4 broadly on Eb4 dorsoposteriorly beginning ventral to OD3–4 insertion on posterior surface of Eb4 just ventral to tip of uncinat process, meeting LP insertion posteriorly; posteroventral edge of insertion meets OP dorsolaterally and Ad4 dorsoanteriorly; Eb4 levator process absent. CT sheet extends from near LE4 and LP insertions to distal end of Eb4 and becomes PP dorsally. ② Like *Polycentropsis* but beginning lateral to OD3–4 insertion on posterior surface of uncinat process and extending laterally to tip of levator process, meeting LP insertion posteriorly; CT sheet begins at levator process.

LP on Eb4 at and anterior to LE4 insertion.

LI1 on lateral edge of dorsoanteriormost tip of Pb2, almost appearing to continue onto adjacent medialmost edge of IAC, and on dorsoanteromedialmost edge of adjacent Pb3. ② Like *Polycentropsis*, but insertion more extensive on Pb2, and, on one side, a few lateralmost muscle fibers continuing onto medialmost surface of IAC.

LI2 on Pb3 dorsoposteriorly immediately medial to medial end of Eb3.

TD comprises TEb2 and TPb3–Eb3, and TEb4. TEb2 muscously continuous only narrowly posteriorly, with mid-anterior notch continuing posteriorly as mid-longitudinal raphe, which gives rise dorsally to CT sheets covering muscles and is continuous anteriorly with CT of pharyngeal roof; ventroanteriorly, muscle attaches loosely to Pb3; laterally muscle attaches on Eb2 dorsally anterior to LE2 insertion; posteriorly muscle is free from TPb3–Eb3. TPb3–Eb3 relatively narrow, begins anteriorly on Pb3 just anterior to medial end of Eb3 and continues posteriorly on posteromedialmost edge of Eb3; muscle is free from TEb4. TEb4 broader than TPb3–Eb3, attaches along Eb4 posteriorly between medial end and uncinat process.

② TD comprises TPb2, TEb2, TPb3–Eb3, and TEb4. TPb2 a semicircular ribbon of muscle on each side, arising ventroanteromedially from TEb2 dorsally and finely attached by CT to dorsoanteriormost surface of Pb3 (not attached to Pb2); muscle curves posterolaterally and joins medial band of CT covering Pb3s posteriorly and joining the bi-lateral muscle straps of TEb2. CT joining muscle sections of TEb2 notched deeply mid-anteriorly; anteriorly joining CT of pharyngeal roof and dorsally giving rise to CT sheets; muscle extends laterally from CT covering Pb3s and attaches on Eb2 dorsally well anterolateral

to LE2 insertion; free from TPb3-Eb3. TPb3-Eb3 ventral to OD3–4, beginning anteriorly a little anterior to LI2 insertion, continuing posteriorly along medial edge of LI2 insertion, and attaching finely to posteromedialmost corner of Eb3; posteriorly continuous by slender, diagonal muscle strand with TEb4. TEb4 slender, on Eb4 a little lateral to cartilaginous medial end, meeting OP dorsomedially.

OD3–4 on Pb3 dorsomedially ventral to TEb2, insertion on Eb3 anteriorly ventral to tip of uncinat process and on Eb4 posteriorly ventral to tip of uncinat process.

OP strap-like; dorsally on Eb4 posteriorly, beginning medially ventral to TEb4 attachment, continuing laterally and meeting LE4 insertion posteriorly, and posteriorly overlapping Ad4 dorsomedially; ventrally on Cb5 dorsoposteriorly, anteriorly meeting TV5 posterolaterally, laterally posteriorly overlapping Ad5 ventromedially. ② Dorsally on Eb4 posteroventrally beginning medially ventral to OD3–4, continuing laterally almost to levator process (lateral to posteroventral edge of LE4 insertion), posteriorly overlapping Ad4 dorsomedially; ventrally like *Polycentropsis*, but joining well-developed raphe with Ad5 posteromedially.

Ad1–3 absent.

Ad4 dorsally on Eb4 beginning ventrally anterior to lateral edge of OP and extending laterally almost to Eb4-Cb4 joint; ventrally on Cb4 dorsally just medial to Eb4-Cb4 joint.

Ad5 strap-like, dorsoanteriorly on Cb4 beginning just medial to distal cartilage tip, posteroventrally on Cb5 beginning just medial to distal cartilage tip. ② Dorsoanteriorly meets Ad4 ventroposterolaterally on Cb4; begins posteroventrally on distal tip of Cb5 and joins raphe with OP ventrolaterally.

SOD absent.

RDs separated by space about one-half diameter of one RD. ② Space less than one-half diameter of one RD.

Additional remarks. SCL attached mid-dorsally to ventral surface of cartilaginous posterior tip of Bb3. TV4 free from Cb5s. Pb2 toothed Pb4 absent; UP4 present.

Afronandus sheljuzhkoii (Meinken), USNM 372183, 65.9 mm.

Plate 138

Description.

LE1 on Eb1 dorsoposteriorly, well lateral to cartilaginous tip of uncinat process; slender ligament originates with LE1 and inserts on Eb1 anteriorly anterior to LE1 insertion.

LE2 on Eb2 about mid-dorsoposteriorly, posterior to posterolateralmost edge of TEb2.

LE3 absent on right side; on left side, a very fine filament inserting on tip of Eb3 uncinat process.

LE4 on Eb4 posteriorly medial to lateral end, anteromedially meeting OD3–4 and laterally meeting LP insertion medially.

LP on Eb4 dorsally beginning at lateral edge of LE4 insertion and extending laterally; CT sheet extends from lateral edge of insertion and becomes PP dorsoposteriorly.

LI1 on Pb2 dorsally just posterior to dorsoanteriormost cartilage tip, insertion becoming tendinous as it joins adjacent anterior end of Pb3; muscle fibers abut medial IAC surface, but no fibers basally insert on IAC.

LI2 narrowly on Pb3 dorsolaterally, medial edge meeting TPb3-Eb3-Eb4 lateral edge.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 broad medial to much narrower extension onto Eb2 dorsally, there attaching anterior to LE2 insertion; broadly, mid-anteriorly consisting of thick CT pad, which attaches anterolaterally to dorsoanteriormost ends of Pb2s and is mid-anteriorly continuous with CT of pharyngeal roof; muscle fibers continuous narrowly and only posteriorly, but interrupted there by very short, fine, mid-longitudinal raphe; muscle not continuous posteriorly with TPb3-Eb3-Eb4. TPb3-Eb3-Eb4 anteriorly ventral to OD3–4s, attaching to Pb3 at medial edge of LI2 insertion, continuing posteriorly and attaching to posteromedialmost corner of Eb3, abruptly narrowing at that point and then expanding considerably and attaching to Eb4 posteromedially, there just reaching dorsomedialmost edge of OP.

OD3–4 origin on Pb3 dorsomedially ventral to TEb2, insertion on Eb3 anteriorly immediately ventral to tip of uncinat process and on Eb4 posteriorly on and ventral to tip of uncinat process; meets LE4 insertion ventroanteriorly.

OP dorsally on Eb4 posteriorly beginning medially near lateral end of TPb3-Eb3-Eb4 and extending laterally to below LE4, overlapping medial half of Ad4 posteriorly; ventrally on Cb5 dorsally beginning near lateral end and extending medially and meeting posterolateral edge of TV5; anteriorly overlapping Ad5 posteromedially.

Ad1–3 absent. GFMsl–3 (not illustrated) moderately well developed.

Ad4 dorsally on Eb4 posteroventrally beginning medially anterior to OP and extending laterally almost to distal end of bony surface; ventrally on Cb4 dorsally beginning medially anterior to OP (which is on Cb5) and extending laterally along Ad5 attachment dorsally to near lateral end of bony surface of Cb4.

Ad5 dorsally on Cb4 posteriorly beginning well medially and extending laterally along ventral edge of Ad4 almost to lateral end of bony surface of Cb4;

ventrally on Cb5 posteriorly beginning near distal end of bony surface and extending medially; overlapped posteriorly by OP.

SOD absent.

RDs almost adjacent.

Additional remarks. SCL present. TV4 free from Cb5s. IAC articulates with cartilaginous medial end of Eb1 uncinat process. Pb4 absent. UP4 present. Eb4 levator process absent on one side, greatly reduced on other (treated as absent).

Monocirrhus polyacanthus Heckel, USNM 103840, 78.1 mm; USNM 269969, cleared and stained, 56.1 mm.

Not illustrated

Description.

LE1 on Eb1 well lateral to tip of uncinat process; strong, ribbon-like ligament originates with LE1 and inserts on Eb1 anteriorly anterior to LE1.

LE2 on raised process on Eb2 posteriorly at about mid-length of element.

LE3 absent.

LE4 broadly on Eb4 dorsoposteriorly beginning lateral to uncinat process and extending laterally much of distance to distal end, laterally meeting slender LP insertion posteriorly.

LP slender, at and anterior to LE4 insertion laterally.

LI1 on Pb2 dorsally just posterior to anteriormost tip, insertion continuing on adjacent anterolateral-most margin of Pb3 and impinging on medialmost surface of IAC, but no fibers basally inserting on it.

LI2 on Pb3 laterally medial to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb3-Eb4. TEb2 muscously continuous from attachment on Eb2 dorsoanteriorly anterior to LE2 insertion on one side across Pbs to attachment to Eb2 on other side; area over Pbs attached mid-ventroanteriorly to pharyngeal roof CT and dorsally to CT sheets, with strongest attachment on each side to muscle surface just medial to extension of muscle onto Eb2; strong CT continues anteriorly, attaching to ventroanterior edge of LI1, and tightly enveloping anterior ends of Pb2 and Pb3 and medial surface of Pb1-Eb1 joint; muscle not continuous with TPb3-Eb3-Eb4. TPb3-Eb3-Eb4 origin ventral to OD3-4, beginning on Pb3 along medial edge of LI2 insertion, continuing onto posteromedial-most corner of Eb3, followed posteriorly by considerable lateral extension, which attaches on Eb4 mid-posteriorly.

OD3-4, OD3' anteriorly on Pb3 dorsomedially ventral to TEb2; OD3-4 posteriorly on bony surfaces of Eb3 uncinat process anteriorly and Eb4 uncinat process posteriorly, almost covering tip of latter process; OD3' branches off OD3-4 ventroanteriorly at

about mid-length and attaches to Eb3 dorsally ventral to OD3-4 on Eb3.

OP dorsally on Eb4 posteriorly beginning medially at about mid-length of Eb4 and extending laterally to below mid-point of LE4 insertion, there joining Ad4 dorsomedialmost edge; ventrally on Cb5 dorsally beginning at posterolateral edge of TV5 and extending laterally a short distance and joining Ad5 postero-medially; not clearly differentiated from SO medially.

Ad1-3 absent.

Ad4 on Eb4 dorsally beginning below about mid-point of LE4 insertion, where Ad4 and OP join, and extending laterally almost to lateral end of bony surface of Eb4; ventrally on Cb4 dorsally beginning medially at point ventral to its medial attachment on Eb4 and extending laterally almost to posterodistal-most end of bony surface of Cb4, meeting Ad5 dorsoan-terolaterally.

Ad5 strap-like, dorsoanteriorly on Cb4 dorsopos-teriorly well medial to lateral end of Cb4, there meet-ing Ad4 and extending medially a short distance; posteroventrally on Cb5 dorsally beginning near dis-tal end and extending a short distance medially, meet-ing OP ventroanteromedially.

Remarks. It is unusual in a perciform for Ad5 to attach well medial to the distal end of Cb4.

SOD absent.

RDs separated by distance about diameter of one RD.

Additional remarks. SCL attached mid-dorsally to tip of posteroventrally extending cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 absent; UP4 present. IAC present. Eb4 levator process absent. Medial end of Eb4 larger than that of Eb3 in 78.1 mm specimen, about equal in 56.1 mm specimen.

SPHYRAENIDAE

Remarks. Johnson (1986) included Sphyraenidae in the Scombroidei, but Orrell et al. (2003 and in preparation) excluded it based on a molecular study.

Sphyraena barracuda (Edwards), USNM 331677, 139 mm.

Plate 139

Description.

LE1 on anterolateral surface of Eb1 uncinat process.

LE2 on raised bony posterior edge of Eb2.

LE3 long tendinous origin, insertion on tip of Eb3 uncinat process.

LE4 long tendinous origin, insertion on dorsal sur-face of Eb4 just lateral to base of uncinat process.

LP medial half of insertion at and anterior to in-sertion of LE4, posterior half is lateral to LE4.

LI1 larger than LI2, broadly on Pb2 dorsoanterior surface beginning at and ventral to TPb2.

LI2 on posterolateral edge of Pb3 anterior to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 dorsal to TEb2, V-shaped, arms anterior, joined posteriorly along mid-longitudinal raphe, which attaches ventrally to CT of pharyngeal roof, each arm attaches to respective Pb2 dorsoanteriormost surface; muscle fuses ventrally with TEb2 on either side of raphe. TEb2 broad, short laterally, attaching to dorsal surface of Eb2 well medial to LE2 insertion, posteriorly continuous by diagonal strap of muscle with TPb3-Eb3. TEb3-Pb3 on Pb3 dorsoposteriorly medial to LI2 insertion and on posteromedial edge of Eb3, free from SOD.

OD3–4 originating on Pb3 anteromedially ventral to TEb2 and inserting on medial edges of Eb3 and Eb4 uncinat processes.

OP relatively slender, dorsally on posterior surface of Eb4 at and medial to uncinat process, ventrally on posterodistal end of Cb5, joining raphe with Ad5 ventrolaterally.

Ad1–3 absent.

Ad4 relatively broad, on Eb4 posteriorly beginning ventral to LE4 insertion and continuing laterally to distal end of bony portion of Eb4, broadly ventrally on Cb4 dorsal surface medial to Eb4-Cb4 joint and medial to broad Ad5 attachment to Cb4.

Ad5 dorsally broadly on posterolateral bony surface of Cb4 just medial to distal end, fusing medially with SO; ventrally broadly on Cb5 laterally, fusing anteriorly with TV5.

SOD present.

RDs separated by space greater than width of one RD. RD extends anteriorly between two longitudinal SO muscle straps: one originating from SO dorsally in region ventral to SOD and extending anteriorly medial to RD and inserting on Pb3 dorsally at and medial to OD3–4 origin, and the other originating in area anterior to OP and extending anteriorly lateral to RD, becoming dorsal to RD anteriorly and inserting on most of medial edge of Pb3 ventral to OD3–4.

Additional remarks. SCL absent (note Bb3 has posteroventrally extending cartilaginous tip which attaches to the ventral aorta where this vessel divides bilaterally and extends anteriorly). TV4 free from Cb5s. Pb4 absent, UP4 present. Pb2 toothed. IAC present. Eb4 levator process absent. Medial end of Eb4 larger than that of Eb3. PCI originates by long tendon on cleithrum and attaches on Cb5 beginning well medial to distal end of Cb5 and continuing medially.

KURTIDAE

Kurtus sp., USNM 345060, 92.4 mm.

Not illustrated

Description.

LE1 on dorsolateral edge of Eb1 uncinat process beginning just lateral to cartilage tip.

LE2 on dorsal edge of expanded posterior margin of Eb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 dorsoposterolateral to tip of uncinat process, ventroposteriorly meeting LP insertion ventroanteriorly.

LP on Eb4 beginning at and extending posterior to LE4 insertion.

LI1 inserting on Pb2 dorsoanteriormost process posteriorly, continuing posteroventrally and attaching to anteriormost edge of Pb3; joining posterior edge of TPb2 attachment to Pb2; smaller than LI2.

LI2 on Pb3 posterolaterally immediately adjacent to medial end of Eb3.

TD comprises TPb2, TEb2, and TEb3. TPb2 roughly V-shaped, arms broad, flat, open anteriorly, completely dorsal to TEb2, with raphe coursing through posterior apex and across TEb2 (thus completely dividing both muscles) and attaching ventrally to dorsomedial edge of each Pb3; muscle attached mid-anteriorly to CT of pharyngeal roof, attached anterolaterally to dorsoanterior tip of Pb2, there joining LI1 just dorsal to its insertion. TEb2 extending laterally and attaching to Eb2 dorsally anterior to LE2 insertion; free posteriorly from TEb3 except for fine posterior CT continuations from dorsomedial edges of Pb3s to mid-longitudinal raphe of TEb3. TEb3 posteroventral to level of TEb2, attaching broadly to posteromedial margin of Eb3; raphe continuing posteriorly across SOD.

OD3–4 origin on Pb3 dorsomedially ventral to TEb2; inserting on Eb3 broadly anteriorly ventral to tip of uncinat process and on Eb4 somewhat less broadly ventral to tip of uncinat process.

OP a relatively narrow strap, dorsally on Eb4 posteriorly beginning medial to uncinat process and extending medially, ventrally on Cb5 dorsally posterior to Ad5, beginning laterally near distal end of Cb5 and extending medially.

Ad1–3 absent.

Ad4 dorsally broadly on Eb4 posteriorly beginning at lateral edge of OP and extending laterally to end of bone, ventrally on Cb4 dorsoposteriorly beginning a little medial to lateral end and anterior to Ad5 attachment and extending medially.

Ad5 dorsally on Cb4 posteriorly beginning near distal end and extending medially, ventrally on Cb5 dorsoposteriorly and extending medially anterior to OP.

SOD very fine, medially with pair of fine ventral extensions from mid-dorsal raphe, each encircling one RD.

RDs separated by distance less than half diameter of one RD.

Additional remarks. SCL interrupted medially by attachment to autogenous ball of cartilage attached to ventral tip of posteroventrally extending cartilaginous posterior end of Bb3 (autogenous ball also present in cleared and stained specimen of *Kurtus indicus*, USNM 305690). TV4 free from Cb5s. Pb4 absent. UP4 present. IAC present. Eb4 levator process absent. Pb1 bony with cartilage tips and, ventrolaterally, uniquely, has toothplate with fine teeth adjoining similar toothplate on medial end of Eb1 (consistent with scale-eating behavior). Pb2 toothed. Medial end of Eb4 smaller than that of Eb3.

The next four families were included with nine others in a suborder Trachinoidei by Nelson (1994: 395 et seq.), who indicated that the composition of the suborder was probably polyphyletic.

AMMODYTIDAE

Ammodytes dubius Reinhardt, USNM 302478, 180 mm.

Plate 140

Description.

LE1 on broad tip of Eb1 uncinete process antero-laterally.

LE2 on tip of raised mid-posterodorsal edge of Eb2.

LE3 on tip of Eb3 uncinete process anteriorly.

LE4 together with LP (laterally) tendinously on dorsal bony edge of Eb4 lateral to uncinete process.

LP together with LE4 (medially) tendinously on bony distal dorsal edge of Eb4 at and lateral to LE4 insertion.

LI1 on bony dorsolateral edge of Pb2 just ventral to articulation with IAC.

LI2 on Pb3 dorsoposteriorly at and lateral to medial edge of Pb3 portion of TPb3-Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 small, thin, V-shaped, dorsal to TEb2 anteriorly, each arm attaching to cartilaginous tip of Pb2 anterior end, junction of arms divided by longitudinal raphe, which continues across TEb2, attached ventrally to CT of pharyngeal roof. TEb2 transversely broad, longitudinally narrow, attaching mid-ventrally to CT of pharyngeal roof, attaching laterally to Eb2 dorsally anterior to LE2 insertion; free and well separated from TPb3-Eb3. TPb3-Eb3 on Pb3 dorsoposteriorly at and medial to LI2 insertion, continuing posteriorly and attaching finely to medial tip of Eb3, continuous mid-posteriorly by crossing strands of muscle with SOD.

OD3–4 origin broadly on Pb3 dorsoposterolateral edge, anteriorly ventral to TEb2, but mostly posterior to TEb2; insertion on Eb3 anteriorly ventral to tip of uncinete process and on medial edge of Eb4 uncinete process.

OP dorsally posteriorly on Eb4 beginning on un-

cinete process and extending laterally almost to beginning of cartilaginous distal end, ventrally on Cb5 dorsolaterally, joining CT ventrolaterally with posterior end of Ad5, medially continuous with SO.

Remarks. This description was completed much earlier than that of *Symphysanodon berryi* (Symphysanodontidae, q.v.), in which the dorsal gill-arch musculature is otherwise remarkably similar. Re-examination of our *A. dubius* specimen indicates the possibility that OP is divided into two parts, similar to *S. berryi*, but this should be verified in another specimen.

Ad1–3 absent.

Ad4 broadly on Eb4 dorsoposteriorly lateral to OP, ventrally on Cb4 beginning at inner angle of Eb4-Cb4 joint and continuing a short distance medially.

Ad5 posteriorly on distal end of Cb5 and anteriorly on Cb4 posterolaterally and AC4 posteroventrally, joining tendinous raphe with OP ventromedially.

SOD present, slender.

RDs separated by distance greater than diameter of one RD.

Additional remarks. SCL attached mid-dorsally to ventroposteriorly extending cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. IAC present. AC4 present (not yet budded off in 111 mm, cleared and stained specimen, USNM 302247). Medial end of Eb3 larger than that of Eb4.

Kayser (1962) described and illustrated the skeleton and musculature of *A. tobianus* Linnaeus. The dorsal gill-arch muscles of *A. tobianus* differ most notably from those of *A. dubius* in that TPb2 is absent, the origin of OD3–4 is completely ventral to TEb2, LI1 and LI2 are much more massive, and AC is apparently absent or has not budded off (thus Ad5 attaches anteriorly only to Cb4). Kayser illustrated the GFMs, which we did not.

TRACHINIDAE

Trachinus draco Linnaeus, USNM 349536, 2 specimens, 80.6–84.3 mm.

Plate 141

Description.

LE1 on Eb1 anteriorly lateral to tip of uncinete process.

LE2 on raised dorsoposterior bony edge of Eb2.

LE3 on tip of Eb3 uncinete process anteriorly.

LE4 on Eb4 dorsoposteriorly between uncinete and levator processes.

LP on Eb4 posterior to LE4.

LI1 on most of Pb2 bony surface dorsomedially with muscle fibers separating dorsoposteriorly and inserting on Pb3 bony surface slightly posteromedial to anterior end of Pb3.

LI2 on Pb3 dorsally medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2

flat, broad, bi-lateral pair of anterolaterally extending muscles originating posteriorly from mid-longitudinal raphe or somewhat heart-shaped ribbon of muscle divided mid-longitudinally; either type dorsally on mid-section of TEb2 and attaching anterolaterally to cartilaginous dorsoanteriormost tip of Pb2; anterior fibers may coalesce medially with those of TEb2; CT sheets attaching to skull arise from mid-longitudinal raphe. TEb2 broad, extending laterally onto Eb2 dorsally anterior to LE2 insertion, not continuous posteriorly with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsolaterally beginning anteriorly medial to LI2 insertion and continuing posteriorly and attaching to posteromedialmost edge of Eb3 (see Remarks following), continuous posteriorly by diagonal muscle strand with SOD.

Remarks. On right side only of larger specimen (illustrated), TPb3-Eb3 continues onto Eb4 dorso-medially. We consider this continuation to be anomalous.

OD3–4 anteriorly on Pb3 dorsomedially ventral to TEb2, posteriorly on anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally on Eb4 posteriorly, extending from uncinat process about half distance to medial end of Eb4, ventrally on Cb5 dorsoposterolaterally.

Ad1–3 absent.

Ad4 broadly dorsally on ventral surface of Eb4 lateral to levator process, ventrally equally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 posterolaterally (reaching distal end), joining raphe with Ad4 ventral attachment; ventrally anterior to OP on Cb5 dorsally, reaching distal end.

SOD present.

RDs separated by space slightly less than diameter of one RD.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. IAC present. Eb4 levator process present.

URANOSCOPIDAE

Kathetostoma cubana Barbour, USNM 187953, 81 mm.

Additional material. ② *Xenocephalus egregius* (Jordan and Thompson), USNM 186212, 89.1 mm.

Plate 142

Description.

LE1 on anterior surface of broad bony flange lateral to tip of Eb1 anterior process (uncinat process and Pb1 absent). ② Uncinat process and tiny Pb1 present.

LE2 short, bulky, on dorsoanterior surface of Eb2 mid-laterally, medial edge of insertion joining raphe with TEb2 lateralmost edge.

LE3 absent.

LE4 long, bulky, on Eb4 dorsoposterolaterally.

LP very fine, at lateralmost edge of LE4 insertion; easily overlooked and lost during dissection.

LI1 on dorsoanterolateralmost surface of Pb3 (Pb2 absent); just dorsoanterior to insertion, attached to thick pharyngeal roof CT enveloping Eb1 medial end and Pb3 dorsoanterior end (dorsoanterior surface of OD3–4 origin also attached to CT medial to LI1; CT thins considerably medially). ② On dorsoanteriormost surface of Pb3 and medial end of small, edentate Pb2; dorsomedialmost edge of insertion attached to CT to which mid-anteromedial edge of TEb2 and anteromedialmost edge of OD3–4 origin also attach; Eb1 medial end not enveloped by same CT; pharyngeal CT not thickened.

LI2 on Pb3 dorsoposteriorly opposite medial ends of Eb3 and Eb4.

TD comprises TEb2 and TPb3-Eb3. TEb2 broad, flat, covering entire Pb area dorsally, with mid-longitudinal raphe giving rise dorsally to CT sheets attaching to skull, attaching mid-ventrally to CT of pharyngeal roof between Pbs; muscle attaches on Eb2 dorsomedially, joining raphe with medial edge of LE2 insertion, and overlies, but is not continuous with, anterior end of TPb3-Eb3. TPb3-Eb3 on Pb3 dorsally medial to LI2 insertion and ventral to OD3–4, continuing on to Eb3 broadly dorsomedially. ② Comprises TEb2, TEb3, and TPb3-UP4. TEb2 broadly continuous posteriorly with TEb3, which attaches on Eb3 dorsally medial to base of uncinat process; TPb3-UP4 completely ventral and weakly attached dorsally to TEb3; muscle attaches on Pb3 posterior edge and adjacent dorsomedialmost edge of UP4, and is continuous posteriorly by diagonal muscle strand with SOD.

OD3–4 origin on Pb3 dorsoanteriormost surface ventral to TEb2, medial to LI1 insertion, and dorsal to LI2 insertion and TPb3-Eb3 anteriorly; dorsoanteriormost surface of muscle strongly attached to thick CT of pharyngeal roof; insertion on medial edges of Eb3 and Eb4 uncinat processes. ② Origin on Pb3 dorsomedially ventral to TEb2; anteromedialmost edge attaches to CT also joined by LI1 and TEb2 (see LI1 above); muscle is dorsal to LI2 insertion and TPb3-UP4 anterolaterally.

OP in two sections: lateral section dorsally on Eb4 posteriorly beginning below LE4 insertion medially and extending medially to below uncinat process, medial section dorsally, narrowly on Eb4 uncinat process, laterally folded over medial section posteriorly (fibers of sections continuous in crotch of fold); both sections attaching together on Cb5 medially and join raphe with PCI dorsoanteriorly (PCI passes between two sections to insert on Cb5); medial section incompletely separated medially from SO. ② Medial section joins tendinous anterior extension of PCI ventroanteriorly and lateral section joins dorsoanteriorly

(also, Ad5 posteriorly joins lateral surface tendon); cartilaginous and adjacent bony area of Cb5 distal end not included in attachments.

Ad1–3 absent.

Ad4 dorsally broadly on Eb4 ventrally below LE4 insertion, ventrally on dorsolateral half of Eb4 medial to Eb4-Cb4 joint; medially, Ad4 attachment on Cb4 is separate from Ad5 attachment on Cb4, but gradually the two muscles meet and distally are inseparable. ② See Ad5.

Ad5 dorsally broadly on Cb4 posterolaterally (see also Ad4), ventrally on Cb5 distally. ② Muscular portion on Cb4 well posteromedial to distal end, but joins CT attaching along posterolateral edge of Cb4; entire muscular portion joins Ad4 ventrally on Cb4; posterior surface joins lateral surface of tendinous anterior end of PCL.

SOD absent. ② Present.

RDs exceptionally large, slightly separated. ② Moderately large, separated by space equal to about half one RD diameter.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1, Pb2, and Pb4 absent, UP4 present. Medial end of Eb4 larger than medial end of Eb3. Eb1 uncinat process absent (see also Rosen and Patterson, 1990, fig. 36b). Eb4 levator process absent.

② Pb1 small, partly bony. Pb2 small, rod-like, edentate. Pb4 absent, UP4 present. IAC absent. Medial end of Eb4 not noticeably larger than that of Eb3. Eb1 uncinat and anterior processes present. Eb4 levator process present, completely covered by LE4 insertion.

Pietsch (1989) hypothesized *Gnathagnus* Gill (junior synonym of *Xenocephalus* Kaup) and *Pleuroscopus* Barnard as the plesiomorphic sister group of a clade including *Kathetostoma* Günther.

CHEIMARRICHTHYIDAE

In a phylogenetic study, Imamura and Matsuura (2003) excluded *Cheimarrichthys* as a close relative of the Pinguipedidae, in which some authors have included it. They were, however, unable to propose a sister-group relationship for *Cheimarrichthys* and recognized it, as have other authors, as the sole member of the Cheimarrichthyidae.

Cheimarrichthys fosteri Haast, USNM 362725, USNM 362725, 71.6 mm.

Not illustrated

(superficially resembles *Callanthias*, Plate 132)

Description.

LE1 on Eb1 uncinat process anteriorly ventral to cartilage tip.

LE2 broadly on Eb2 dorsoposteriorly, medial edge meeting posterolateral end of TEb2.

LE3 broadly on Eb3 anteriorly, beginning at tip of uncinat process and extending laterally.

LE4 largest levator, on Eb4 dorsolaterally, reaching distal end of bony surface, posterolaterally joining LP insertion.

LP on Eb4 at and lateral to LE4 insertion.

LI1 on Pb2 dorsomedially and adjacent anterior end of Pb3, there meeting OD3–4 anteromedially.

LI2 on Pb3 posterolaterally, medial edge of posterior half of insertion meeting TPb3-Eb3.

TD comprises TEb2 and TPb3-Eb3. TEb2 band-like with mid-longitudinal raphe, which attaches ventrally to pharyngeal roof CT and anterior edge of TPb3-Eb3, muscle extends laterally to point anterior to LE2 insertion. TPb3-Eb3 band-like attaching on Pb3 posterolaterally beginning anterior to LI2 insertion, continuing along medial edge of LI2 insertion, and attaching to posteromedialmost corner of Eb3; continuous posteriorly by diagonal muscle strap with SOD.

OD3–4 broadly, anteriorly on Pb3 dorsomedially, meeting LI1 posteriorly; posteriorly on medial edges of Eb3 and Eb4 uncinat processes.

OP thick, strap-like; dorsally on Eb4 uncinat process posteriorly, there meeting OD3–4, and extending laterally to below medial end of LE4 insertion, which it also meets, and, at that point, overlaps dorsomedial half of Ad4 posteriorly; ventrally on Cb5 posteriorly beginning laterally at posteroventral end of Ad5 and extending medially for distance about equal to extent on Eb4; medially clearly differentiated from SO on one side, unclearly on the other.

Ad1–3 absent.

Ad4 dorsally on Eb4 posteriorly, beginning medially anteroventral to OP and extending laterally to distalmost end of bony surface; ventrally on Cb4 dorsally beginning medially ventral to a perpendicular from dorsomedial origin on Eb4 and extending laterally to distalmost end of bony surface, meeting Ad5 anteriorly for most of latter's length.

Ad5 short, anteriorly on Cb4 posterodistal edge, meeting Ad4, posteriorly on Cb5 dorsally, beginning medially a little anterior to OP ventrolaterally and ending near distalmost end of bony surface.

SOD present.

RDs separated by space equal to about one RD diameter.

Additional remarks. SCL present, apparently free from ventrally curving cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb1 short, cartilaginous, oriented medially (horizontally). Pb2 toothed. Eb4 levator process absent. IAC present.

Scorpaenoidei

Imamura and Yabe (2002) hypothesized a reorganization and recomposition of the Scorpaeniformes

of previous authors. They recognized a scorpaenoid-serranoid sister group, on the one hand, and a zoarcoid-cottoid sister group on the other. They did not imply that the two sister groups are closely related, but assigned both to the Perciformes. Furthermore, they excluded the Champsodontidae and Normaniichthyidae as possible members of either of the two sister groups.

We retain the scorpaeniform composition of earlier studies in our arrangement of the taxa that follow, but treat the group as a suborder. We do so only for convenience and absent of intent to imply judgment on Imamura and Yabe's study. In fact, see additional remarks following the description of *Hexagrammos stelleri*, Hexagrammidae.

SCORPAENIDAE

Pontinus rathbuni Goode and Bean, USNM 190360, 90.8 mm.

Plate 143

Additional material. ② = *Neomerinthe beanorum* (Evermann and Marsh), USNM 187913, 80.6 mm.

SEBASTIDAE

③ = *Sebastes proriger* (Jordan and Gilbert), USNM 1066601, 106 mm.

Not illustrated

Description.

Remarks. Ishida (1994) hypothesized the phylogeny of the scorpaenoid fishes, in which he described various aspects of the dorsal gill-arch musculature. He hypothesized that the Sebastidae are the sister group of all other scorpaenoids. We noted few trenchant differences in the muscles of the three genera of scorpaenoids we examined, although some cartilaginous elements of the gill arches exhibit differences. We illustrate *Pontinus* because our preparation was much better than those of the other two genera.

LE1 origin tendinous, insertion on base of Eb1 uncinat process anteroventrally. ② Origin not observed. ③ Origin muscular. ② ③ Insertion on Eb1 uncinat process anterolaterally.

LE2 on Eb2 mid-dorsoposteriorly.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on medial bony edge of Eb4 levator process.

LP at and lateral to LE4 insertion, just extending onto tip of levator process.

LI1 broadly on Pb2 dorsoanterior process beginning just posterior to dorsal tip, attaching to CT joining medial edge of process to adjacent surface of Pb3 dorsoanterior process (medial edge of Pb2 process, where LI1 inserts, just overlaps lateral edge of Pb3 process); ventral surface of muscle fans out posteriorly toward insertion such that in dorsal view it appears that there is a separate dorsoanterior insertion

overlying a ventroposterior insertion along medial edge of Pb2 process. ② Insertion more restricted, but muscle inserts on both Pb2 and Pb3. ③ Insertion does not fan out ventrally, insertion area relatively about half that of *Pontinus*.

LI2 on Pb3 dorsoposterolaterally at lateral edge of TPb3 and medial to medial end of Eb3.

TD comprises TPb2, TEb2, TPb3-Eb3-Eb4. TPb2 centrally oblong with mid-anterior and mid-posterior notches joined by mid-longitudinal raphe, which gives rise dorsally to CT sheets attaching to skull; attached anterolaterally to dorsoanteriormost surface of Pb2 (with weak CT strands attaching to dorsoanteriormost tip of Pb3); attached anteriorly to CT of pharyngeal roof between dorsoanterior ends of Pb2s; muscle lying dorsal to all but small posterior portion of TEb2, ventrally joining with TEb2 along mid-longitudinal raphe and fusing with TEb2 posteromedially on left side (less so on right side). TEb2 mostly ventral to posterior half of TPb2 and joining TPb2 along mid-longitudinal raphe, muscle attaching on Eb2 dorsally well medial to LE2 insertion; well separated (possibly anomalous) from TPb3 posteriorly. TPb3-Eb3-Eb4 broadly dorsolaterally on Pb3, joining medial edge of LI2 insertion, fine, tendinous attachment to medial end of Eb3 on one side and posteromedialmost bony edge of Eb3 on other, broadly on Eb4 dorsoanterior surface well medial to uncinat process, continuous mid-posteriorly with slender SOD. ② ③ TPb2 unnotched posteriorly, completely dorsal to central part of TEb2; TEb2 continuous posteriorly by fine strands of muscle with TPb3-Eb3-Eb4; fine, tendinous attachment to medial end of Eb3 in both taxa.

OD3-4 origin on dorsoanterior surface of Pb3 ventral to TEb2, insertion on dorsoanterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally beginning on Eb4 uncinat process posteriorly and extending laterally to posteroventral surface of levator process, there meeting Ad4; ventrally broadly on Cb5 dorsoposteriorly, overlapping Ad5 ventroposteriorly; indistinguishable from SO medially.

Ad1-3 absent.

Ad4 continuous sheet beginning dorsally on ventral surface of Eb4 levator process and continuing laterally to Eb4-Cb4 joint, from there attaching dorsally along lateral third of Cb4, meeting Ad5 narrowly dorsally on Cb4 ventral to Eb4-Cb4 joint.

Ad5 dorsally narrowly meeting Ad4 on Cb4 posterior surface medial to distal end, ventrally on Cb5 dorsodistally anterior to OP attachment.

SOD slender.

RDs separated by space equal to about half diameter of one RD. ② Separated by space equal to

about diameter of one RD. ③ Separated by space more than twice diameter of one RD.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. IAC attached by loose ligament to Pb2. ② IAC attached directly to Pb2. ③ IAC attached directly to Pb2; AC4 present.

PLATYCEPHALIDAE

Platycephalus endrachtensis Quoy and Gaimard, USNM 173884, 113 mm.

Plate 144

Additional material. ② = *Inegocia japonica* (Tilesius), USNM 99761, 67.3 mm.

Description.

LE1 on Eb1 dorsally anteroventral to uncinate process.

LE2 on dorsally expanded posterior margin of Eb2 anteriorly.

LE3 on Eb3 uncinate process anteriorly. ② Absent.

LE4 on Eb4 levator process dorsally just medial to cartilaginous edge.

LP insertion fused anteroventrally with posteroventral edge of LE4 insertion.

LI1 on Pb2 dorsomedially, continuing medially along anterolateralmost edge of Pb3 adjacent to Pb2; little, if any, larger than LI2.

LI2 on Pb3 dorsoposteriorly, medial edge of attachment meeting lateral edge of TPb3-Eb4.

TD comprises TEb2 and TPb3-Eb4. TEb2 broad with mid-longitudinal raphe giving rise dorsally to filmy CT sheets covering muscles; anterolateral and posterolateral muscle fibers coming together and attaching to Eb2 dorsally anterior to LE2 insertion; muscle continuous posteriorly by fine diagonal muscle strand with TPb3-Eb4. TPb3-Eb4 on Pb3 dorsally meeting medial edge of LI2 insertion; muscle fibers extend dorsomedially joining ventral surface of Eb4 portion of muscle, which extends well laterally and inserts on Eb4 dorsally between medial end and surface ventral to uncinate process; on one side, an apparently anomalous muscle strand of Eb4 portion inserts on dorsomedialmost bony surface of Eb3; muscle continuous posteriorly by fine diagonal muscle strand with SOD. ② Comprises TEb2 and TPb3-Eb3; TEb3 on Eb3 mid-posteriorly.

OD3–4 origin finely on Pb2 anteriorly, continuing broadly on entire dorsomedial edge of Pb3; insertion broadly on anteromedial edge of Eb3 uncinate process and posterior surface of Eb4 uncinate process. ② On Pb2 and Pb3 on one side, but only on Pb3 on other.

OP dorsally on Eb4, extending medially from ventral surface of levator process to posterior surface of uncinate process, ventrally on Cb5 dorsoposteriorly, medially continuous with SO.

Ad1–3 absent.

Ad4 in two sections; anterior section broadly dorsally on Eb4 ventrally lateral to OP, ventrally broadly on Cb4 dorsally anterior to posterior section; posterior section about half as broad as anterior section, fibers angled ventrolaterally (versus almost vertical for anterior section), dorsally on ventral surface of Eb4 levator process, ventrally on Cb4 dorsally posterior to anterior section, joining raphe with Ad5 on Cb4. ② Consists of anterior section only.

Ad5 dorsally on posterolateral bony surface of Cb4 well medial to distal end, joining raphe with Ad4; ventrally on bony surface of Cb5 dorsolaterally, joining raphe posteriorly with OP ventroanteriorly.

SOD present.

RDs separated by distance greater than diameter of one RD.

Additional remarks. SCL attached mid-dorsally by CT to tip of posterior cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb1 mostly bony. IAC present (see discussion below). Medial end of Eb3 larger than that of Eb4. Pb2 toothed. ② Pb4, if present, greatly reduced. IAC absent.

Platycephalus appears to be more plesiomorphic than *Inegocia* in having IAC, LE3, and Pb4, and more specialized, perhaps, in having TD attaching to Eb4. Only *Platycephalus* is included in the cladistic analysis.

Imamura (1996) published a phylogenetic analysis of the Platycephalidae and related taxa. He described the dorsal gill-arch musculature (1996:172–173) of platycephalids in general, provided a generalized illustration (1996:fig. 43) of this musculature in the platycephalid *Sorsogona tuberculata* Cuvier, and discussed variation he found in other platycephalid taxa. In so far as they are comparable, our findings agree with his.

Imamura (1996:132–133) also illustrated and reported briefly on the gill-arch muscles of the Bembridae and Hoplichthyidae, outgroup families most closely related to the Platycephalidae. He illustrates (but does not label) the most plesiomorphic of these, Bembridae, as having or lacking TPb2 (depending on genus), which muscle he reports is lacking in Hoplichthyidae and Platycephalidae.

CHAMPSODONTIDAE

Champsodon atridorsalis Ochiai and Nakamura, USNM 297752, ca. 94 mm.

Additional material. USNM 297752, ca. 82 mm; *C. vorax* Günther USNM 122578, 126 mm, partial in situ dissections to determine presence of LP, q.v.

Not illustrated

Description.

Remarks. Mooi and Johnson (1997) present a detailed morphological description of *Champsodon vor-*

ax, which is representative of the genus. We agree with most of their description of the dorsal gill-arch muscles, but expand on it and note a few differences.

LE1 broadly on Eb1 dorsally well lateral to tip of uncinat process, beginning near point of anteriorly deflected (normally medially directed) arm of Eb1 (see Mooi and Johnson, 1997:fig. 8b for dorsal gill-arch skeletal structure).

LE2 on apex of prominent, raised Eb2 triangular process.

LE3 slender, on tips of joined Eb3 and Eb4 uncinat process anteriorly.

LE4 largest levator, on Eb4 dorsoposteriorly.

LP very fine, fragile, origin near dorsoanteriormost edge of PP, insertion on Eb4 co-incident with ventrolateralmost edge of LE4 insertion.

Remarks. Mooi and Johnson (1997:152) reported LP absent, which VGS verified (*ibid.*, p. 174), based on what now appears to have been a defective dissection. LP is often fragile and destroyed in acanthomorphs unless special care is taken to ascertain its presence early during dissection while the levators are still attached at both their origins and insertions.

LI1 on Pb3 dorsally beginning just posterior to anteriormost tip.

LI2 on Eb3 posteriorly a little lateral to medial end, penetrates OD3–4 on way to insertion.

Remarks. *Champsodon* is the only taxon we encountered in which LI2 inserts exclusively on an Eb. In percomorphs, LI2 usually inserts on Pb3 at, or occasionally ventral, to articulation of Pb3 with Eb3, and it is possible that we have overlooked the fact that some LI2 filaments might be associated with the distal end of Eb3. Penetration of OD3–4 by LI2 occurs uncommonly in acanthomorphs (e.g., *Brotula*, Ophidiidae, and related *Calomopteryx*, Bythitidae; synapomorphic for gobioid family Odontobutidae).

TD comprises a modified TPb2 and TEb2 (together with continuous mid-longitudinal raphe), and TEb4 (no raphe). TPb2 in three parts: anterior part a broad, transversely continuous strap attaching anterolaterally to tip of Eb1 uncinat process and adjacent IAC dorsomedially, also weaker attachments to adjacent dorsal edges of anteriormost tips of Pb2 and Pb3; posterior two parts (one on each side) each consisting of slender muscle slip arising from surface of TEb2 lateral to mid-longitudinal raphe and curving anterolaterally before finely, tendinously joining short raphe extending posteriorly from attachment of anterior TPb2 part to Eb1; anteroventral edge of LI1 also finely joined to same raphe, which marks shallow constriction between anterior TPb2 part and TEb2; TPb2 otherwise broadly continuous posteriorly with TEb2. TEb2 a broad, transversely continuous muscle strap narrowing laterally and twisting as it passes between LI1 and LI2 and attaches on TEb2 dorsally anterior to LE2 insertion; TEb2 posteriorly

is free from and dorsal to anterior edge of TEb4. TEb4 attaches broadly on posterior edge of Eb4.

Remarks. TPb2 is unusual but readily derivable from a common acanthomorph TPb2 muscle state in which TPb2 consists of a depressed, roundish pad dorsal to and continuous partially or completely ventrally with TEb2. Reduction of much of the pad, leaving only its lateral edges and anterior portion would result in the condition found in *Champsodon*. In some acanthomorphs (e.g., *Psenopsis*, Plate 177) only the anterolaterally curving portion of TPb2 is present. The attachment of TPb2 to the tip of Eb1 uncinat process appears to be concomitant with a reduction in size and ventral displacement of IAC, which, unusual for an acanthomorph, articulates with the bony surface of the Eb1 uncinat process ventral to its cartilage tip. While not common among acanthomorphs, TPb2 may attach well out on the dorsal surface of IAC (e.g., *Pseudupeneus*, Plate 124).

OD3–4 originates very broadly on Pb3 dorsomedially and inserts on Eb3 anteriorly ventral to tip of uncinat process and Eb4 posteriorly ventral to tip of uncinat process; muscle penetrated by LI2 (see remarks following LI2).

OP dorsally on Eb4 posteroventrally (slightly ventral to level of SO attachment on Eb4), beginning medially ventral to LE4 insertion and extending laterally and meeting Ad4 dorsomedially; curving strongly ventromedially and attaching on Cb5 narrowly posteriorly medial to posterior end of Cb5; mid-medially not clearly differentiated from SO.

Remarks. Mooi and Johnson (1997:fig. 12a) do not differentiate OP and Ad4 from SO.

Ad1–3 absent.

Ad4 dorsally on Eb4 ventrally beginning medially at lateral edge of OP and extending laterally almost to distalmost end of bony Eb4 surface, attaching ventrally on Cb4 dorsally, meeting entire edge of Ad5 attachment on Cb4.

Ad5 relatively long, dorsoanteriorly on Cb4 beginning medial to distal end and continuing medially on Cb4 for about half length of Ad5, joining raphe with Ad4 attachment on Cb4; posteroventrally on Cb5 dorsally beginning at distal end and extending medially a short distance, meeting OP insertion.

SOD absent.

RDs separated by about diameter of one RD.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. Eb4 levator process absent.

HEXAGRAMMIDAE

Hexagrammos stelleri Telesius, USNM 130279, 2 specimens, 119–123 mm.

Plate 145

Description.

LE1 on raised posterior surface of Eb1 dorsally lateral to tip of uncinat process.

LE2 on Eb2 mid-dorsoposteriorly, meeting distal end of posterior branch of TEb2 anteriorly and, on right side only, meeting distal end of anterior branch posteriorly (fails anteriorly to meet TEb2 posteriorly on left side).

LE3 on Eb3 just anteroventral to tip uncinat process.

LE4 on Eb4 dorsoposteriorly lateral to uncinat process, ventrolateral margin of insertion joined by LP.

LP on Eb4 dorsolaterally, joining LE4 insertion ventrolaterally and extending laterally to dorsodistalmost bony end of Eb4.

LI1 extends ventrally between overlapping anterior ends of Pb2 (anteroventral) and Pb3 (posterodorsal), inserting almost entirely on Pb3 ventroanteriorly, including dorsoanteromedial edge of anterior end of Pb3 dorsal to dorsoanteriormost origin of OD3–4 on Pb3; a few fibers insert on Pb2 dorsolateral surface.

LI2 on Pb3 dorsoposteriorly just medial to medial end of Eb3; posterior half of medial edge of insertion meets lateral edge of TPb3-Eb3 attachment on Pb3.

TD comprises TEb2, TPb3-Eb3, and, questionably, TPb2 (see remarks following TD description). TEb2 medially broad, notched mid-posteriorly, with irregular mid-longitudinal raphe attaching dorsally to filmy CT sheets and ventrally to CT of pharyngeal roof; medial portion lies dorsal to, and extends well anterior to, all Pbs except Pb1; dorsolateral margin on each side of central portion forms fine, flat muscle ribbon, which unites anteromedially and posteromedially with remainder of muscle; muscle narrows and extends laterally, dividing and attaching on Eb2 dorsally anterior and posterior to LE2 insertion (see also LE2); few fine muscle strands join heart-shaped portion posteroventrally to mid-anterior edge of TPb3-Eb3 (strands not visible in dorsal view). TPb3-Eb3 on Pb3 dorsoposteriorly joining posterior half of LI2 insertion medially and continuing posteriorly onto Eb3 dorsomedially; posteromedially continuous by diagonal muscle strands with SOD.

Remarks. Shinohara (1994:50) illustrated the dorsal gill-arch musculature of the hexagrammid *Pleurogrammus azonus* Jordan and Metz. The illustration appears generalized, and he reported no variation in the muscles either among hexagrammids or between hexagrammids and his comparative material. His report that TDA includes attachment to Eb4 is not true of our specimens of *H. stelleri* (a species included in his material), nor is his report that LI1 inserts [only] on Pb2. The extent to which unexplored variation probably exists in his comparative material should be obvious from the variation in muscles often reported in the present study.

He faintly indicates a fine circular perimeter of muscle fibers on a central differentiated plate-like muscle section between the right and left “arms” of what is clearly TEb2, but does not label or describe it.

Imamura and Yabe (2002:fig. 14A) illustrate the dorsal gill-arch musculature of *Hexagrammos lagocephalus* (Pallas), which, insofar as can be told, appears mostly similar to ours of *H. stelleri*. It differs in having TPb2 well-developed and unambiguous and in indicating that the attachment of TEb2 to Eb2 is only anterior to LE2 insertion, which may be an oversight.

Based on Imamura and Yabe’s illustration, we recognize the presence of TPb2 in our specimen of *H. stelleri*.

OD3–4 originating broadly on posteroventral shelf of Pb3 and inserting on joined Eb3 and Eb4 uncinat processes medially; dorsoanteriorly, origin meets LI1 insertion on Pb3.

OP dorsally on Eb4 posteriorly beginning medially on uncinat process, meeting OD3–4 there in a raphe, and continuing laterally to point ventral to LE4 insertion; ventrally, broadly on Cb5 dorsally, meeting and narrowly joining ventrolateral end of Ad5 on dorsodistalmost end of Cb5.

M. SO-Pb3 absent.

Ad1–3 absent; fine GFM on anterolateral surfaces of Eb1 and Cb1, and anterolateral edges of Eb2 and Cb2, and Eb3 and Cb3.

Ad4 dorsally on Eb4 posteroventrally, beginning just medial to lateral edge of OP and extending laterally to Eb4-Cb4 joint, ventrally on Cb4 broadly anterior to Ad5.

Ad5 dorsally on Cb4 beginning posterodistally and extending a short distance medially, ventrally, narrowly on Cb5 dorsally, mostly anterior to OP.

SOD present.

RDs adjacent or narrowly separated, inserting on Pb3 posteriorly.

Additional remarks. SCL present. TV4 free from Cb5s. IAC reduced to one or two small cartilages contained in ligament attaching Eb1 uncinat process to Pb2. Pb4 and UP4 present. Pb1 cartilaginous. In a C&S specimen of *H. superciliosus* (Pallas), USNM 290478 (ca. 135 mm SL), Pb1 is cartilaginous on one side and ossified, with cartilaginous dorsal and ventral ends, on the other. Eb4 levator process absent.

The attachment of TEb2 to Eb2 both anterior and posterior to LE2 insertion was otherwise encountered only in Imamura and Yabe’s (2002:fig. 14B) illustration of *Pholis nemulosa*. Another similarity of *H. stelleri* to *Pholis* is that both have cartilaginous Pb1s. The ligament attaching Eb1 uncinat process to Pb2 in *Pholis* appears similar to that of *H. stelleri*, except that the latter has a couple of small pieces of cartilage representing IAC included in the ligament.

We believe that the TEb2 attachment, and probably the interarcual ligament and cartilaginous Pb1, supports Imamura and Yabe's (2002) hypothesis of a sister-group relationship between their cottoid and zoarcoid lines.

ANOPLOPOMATIDAE

Anoplopoma fimbria (Pallas), USNM 269910, 149 mm.

Not illustrated

Description.

LE1 on Eb1 dorsoposteriorly a little medial to mid-length.

LE2 on Eb2 dorsoposteriorly a little lateral to mid-length.

LE3 on Eb3 just ventral to tip of uncinate process.

LE4 on Eb4 dorsally somewhat medial to distal end, meeting LP insertion anteriorly.

LP on Eb4 dorsally at bony posterior edge at medial end of thin cartilaginous extension of distal cartilaginous tip of Eb4, meeting LE4 insertion posteriorly.

LI1 on Pb2 broadly anterodorsally and extending posteriorly on anterolateralmost edge of Pb3.

LI2 on Pb3 dorsoposterolaterally medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 not attached to Pb2, comprises two flat, semi-circular bands dorsal to TEb2 mid-section, which floors space between bands; muscle confluent mid-laterally with TEb2; anteriorly and posteriorly joining mid-longitudinal raphe which gives rise dorsally to CT sheets covering muscle and is attached mid-ventrally to CT of pharyngeal roof. TEb2 extends laterally and attaches on Eb2 anteriorly a little lateral to LE2 insertion, muscle not continuous posteriorly with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsolaterally ventral to OD3–4, beginning along medial margin of LI2 insertion and continuing posteriorly and joining medialmost edge of Eb3, broadly continuous posteriorly with SOD.

OD3–4 origin broadly on Pb3 dorsoanteriorly, posteriorly on Eb3 anteriorly beginning just ventral to tip of uncinate process, meeting LE3 insertion, and on Eb4 posteriorly beginning just ventral to tip of uncinate process.

OP stringy, infiltrated with amorphous CT, beginning dorsally on Eb4 ventral to LP insertion and extending medially to attachment of OD3–4, broadly overlapping Ad4 medially; ventrally on Cb5 beginning dorsodistally posterior to Ad5 and extending medially a short distance.

Ad1 muscle flat, beginning narrowly on anterior surface of lateral quarter of Eb1, fanning out laterally and covering Eb1–C1 joint; not as well-developed relatively as Ad1 of other fishes, but better developed

than most GFM1s; it and Ad2 and Ad3, possibly should be treated as GFMs.

Ad2 similar to Ad1, but muscle extends medially on Eb2 and meets distal end of TEb2.

Ad3 similar to Ad1, but muscle extends medially to medial end of bony surface.

Ad4 dorsally broadly on Eb4 posteriorly, beginning medially near about medial margin of OP and extending laterally to axilla formed by posteriorly extending (but medial in orientation) cartilaginous process on distal end of Cb5 and main portion of cartilaginous distal end; ventrally much more narrowly on Cb4 medial to angle formed by Cb4 and Eb4.

Ad5 relatively short, ventrally on Cb5 dorsodistally anterior to OP, dorsally on Cb4 distally ventral to posteriorly extending cartilaginous process (see Ad4).

SOD broad.

RDs robust, barely separated from each other.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 and UP4 present. Pb1 absent (anterior process absent). Pb2 toothed. IAC absent. Medial end of Eb4 smaller than that of Eb3. Eb4 levator process absent. PCI begins a little medial to distal end of Cb5 and extends well medially.

There is a remarkable similarity of the gill-arch muscles of *Anoplopoma* and the zoarcoid *Bathymaster*.

RHAMPHOCOTTIDAE

Rhamphocottus richardsonii Günther, USNM 49141, 57 mm.

Plate 146

Description.

LE1 on Eb1 lateral to broad uncinate process.

LE2 on Eb2 mid-dorsoposteriorly.

LE3 absent. (See additional remarks.)

LE4 on Eb4 dorsoposterolaterally medial to distal end, meeting LP insertion medially.

LP at and lateral to LE4 insertion.

LI1 partially on Pb2 dorsoanteriorly, but mostly on dorsoanteriormost surface of Pb3, joining raphe medially with OD3–4 origin present).

LI2 on Pb3 dorsolaterally just medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 a bilateral pair of laterally convex muscle straps, not attached to any skeletal element (muscle usually attaches to Pb2 in acanthomorphs), arising broadly, seamlessly anteriorly and posteriorly from TEb2. TEb2 broadly oblong mid-dorsally with mid-longitudinal raphe giving rise dorsally to filmy CT; muscle attaching beginning mid-anteroventrally and continuing posteriorly, to CT of pharyngeal roof; attaching laterally on Eb2 dorsoanteriorly anterior to LE2 insertion; overlapping anterior end of, and posteroventrally

trally continuous by fine muscle strands with, TPb3-Eb3. TPb3-Eb3 on Pb3 dorsoposterolaterally medial to medial end of Eb3 and ventral to attachment on dorsomedial end of Eb3, broadly continuous posteriorly with SOD.

OD comprises OD3-4 and OD3'. OD3-4 origin broadly on Pb3 dorsomedially, branching ventrolaterally almost immediately into short OD3' (not illustrated), which inserts on medial end of Eb3 dorsally, and OD3-4, which inserts on Eb3 uncinat process anteriorly and Eb4 uncinat process medially.

Remarks. OD3' usually attaches to Eb3 dorsally ventral to OD3-4 or OD3 attachment to anterior surface of Eb3 uncinat process.

OP dorsally on Eb4 posteriorly beginning on posterior bony surface of uncinat process and extending laterally to below mid-insertion of LE4, ventrally on Cb5 posterolaterally, joining raphe ventrolaterally with Ad5, inseparable medially from SO.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteriorly beginning below medial end of insertion of LE4 and extending laterally to Eb4-Cb4 joint, ventrally on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 well medial to distal end, ventrally on Cb5 dorsodistally.

SOD very broad.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 absent. IAC absent. Eb4 levator process absent.

Yabe (1985) described the dorsal gill-arch musculature of cottoids and various related taxa. He hypothesized *Rhamphocottus* as the sister group of all other cottoids. Although his gill-arch muscle descriptions are generalized, we agree with him that there is limited variation in these muscles. Yabe reported, however, that the absence of LE3 is a synapomorphy of cottoids, although in some taxa a few strands of LE4 attach to Eb3. We found LE3, varying from well developed to moderately reduced in all three species of *Myoxocephalus* we examined, two of which were also included in Yabe's material (see *Myoxocephalus*, Cottidae). The presence of LE3 in *Myoxocephalus* is either autapomorphic for the genus among cottoids, or more widely distributed among cottoids than Yabe noted.

Yabe and Uyeno (1996) repeated Yabe's (1985) cottoid synapomorphies in excluding *Normanichthys crockeri* (Normanichthyidae) from among the cottoids.

COTTIDAE

Myoxocephalus niger (Bean), USNM 70823, 2 specimens, 83.8 mm (second specimen, 89.2 mm, ex-

amined only for presence of LE3, LE4, LP); *M. jaok* (Cuvier), USNM 127057, ca. 130 mm, and *M. stelleri* Tilesius, USNM 54232, 94.7 mm (both examined only for presence of LE3, LE4, LP). ② = *Cottus carolinae* (Gill), USNM 163051, not measured.

Not illustrated

Description.

LE1 dorsoposterolaterally on Eb1 uncinat process. ② On Eb1 lateral to uncinat process.

LE2 dorsoposteriorly on Eb2 at about mid-length. ② Near distal end of Eb2 dorsoposteriorly.

LE3 well developed, dorsoposteriorly on Eb3 slightly lateral to tip of uncinat process. ② Absent. (See also additional remarks under *Ramphocottus* (Ramphocottidae).)

LE4 broadly on posterodorsal surface of Eb4 lateral to uncinat process.

LP on posterodorsal surface of Eb4 at and posterior to LE4 insertion.

LI1 has split insertion: on dorsoanterolateralmost edge of Pb3 (along origin of OD3-4 anterolaterally) and on ventroanterior surface of Pb3 sandwiched between Pb3 and dorsoanterior surface of Pb2. ② Similar, but Pb2 is absent.

LI2 on Pb3 dorsal surface ventral to OD3-4 and anterior to medial end of Eb3.

TD comprises TEb2 and TEb3. TEb2 attached anteroventrally to CT dorsal to LI1 and along ventral midline to CT of pharyngeal roof; mid-longitudinal raphe dorsally giving rise to filmy CT sheets; attaching laterally on Eb2 dorsally anterior to medial end of LE2 insertion; faint indication dorsally on one side of laterally curving muscle fibers overlying main portion of muscle laterally (possible vestigial remnant of TPb2); continuous by fine strand of muscle posteriorly with TEb3. TEb3 very narrow, finely, tendinously attaching to Eb3 about one-fourth length lateral to medial end; posteriorly continuous with SOD. ② Mid-longitudinal raphe is continuous on anterior portion of TEb3; TEb2 extends laterally to opposite LE3 insertion, is broadly continuous with, and overlaps slightly, anterior end of TEb3; no indication of TPb2 fibers; TEb3 attaches muscously to the medial end of Eb3.

OD3-4 origin on dorsoanterior surface of Pb3, insertion on medial edges of Eb3 and Eb4 uncinat processes.

OD3' origin on Pb3 dorsoanteriorly ventral to OD3-4, insertion on Eb3 anteromedial surface. ② Muscle not distinct, represented as muscle fibers originating on Pb3 immediately medial to OD3-4 insertion and inserting on medial end of Eb3 at and ventral to TEb3 attachment. (See remarks following OD3' in *Rhamphocottus*).

OP broadly dorsally on posterior surface of Eb4

uncinate process and extending laterally to below mid-insertion point of LE4, ventrally on Cb5 dorso-laterally, joining raphe there with Ad5; only slightly separated dorsolaterally from Ad4. ② Distinctly separated from Ad4.

Ad1–3 absent.

Ad4 dorsally on Eb4 posterolaterally, ventrally joining raphe with Ad5 on Cb4 dorsolaterally. ② Ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 posterior surface beginning about one-fourth length from lateral end and extending medially to point a little past mid-length of Cb4, ventrally on Cb5 dorsodistally. ② Dorsally on Cb4 a little medial to distal end, ventrally on distal end of Cb5 dorsolaterally.

SOD broad.

RDs adjacent. ② RDs separated by space equal to about half width of one RD.

Additional notes. SCL attached mid-dorsally to ventrally extending cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb4 and UP4 absent.

NORMANICHTHYIDAE

Normanichthys crockeri Clark.

Not illustrated

Remarks. Specimens unavailable. See Yabe and Uyeno (1996) for anatomical description and illustrations. Information below extracted from their study and modified to be consistent with present study. Figures mentioned are theirs. Although they excluded *Normanichthys* as having close cottoid relationships, Yabe and Uyeno were unable to propose a reasonable sister group for it. They assigned it as incertae sedis to Scorpaeniformes on the sole basis that it has a suborbital stay.

LE1, LE2, LE3, LE4, LP present.

LI1 on anterior margin of Pb2.

LI2 on dorsolateral margin of Pb3.

TEb2 present [TPb2 absent, based on their fig. 7c]. An additional transversus of undescribed attachments present posteriorly.

OD3–4 originating on Pb3 dorsally, inserting broadly on Eb4, some fibers inserting on “dorsal process” of Eb3.

OP not described, but present in fig. 7c.

Ad1–4 present (fig. 8).

Ad5 joins Cb5 and Eb4.

SOD not described, but present in fig. 7c.

RDs separate, inserting on dorsomedial margin of Pb3 (fig. 3c).

Slender, muscular SO branch [modified CPb?] extending anteriorly lateral to Pb4 [= UP4?] and Pb3 and attaching to posterolateral corner of Pb2. [See their fig. 3b]. This muscle differs from M. SO-Pb2 in that the latter passes medial to UP4 and Pb3.

SCL present (see their fig. 7b, but not labeled). TV4 apparently undivided. Pb1 and IAC absent. Pb2 toothed. Pb4? UP4 present. Uncinate and levator processes not described. Their fig. 3c illustrates an all bony Eb3 uncinat process and no indication that Eb4 has either an uncinat or levator process.

Carangoidei

Although Freihofer (1978) first noted a synapomorphy uniting the four families of carangoid fishes, Smith-Vaniz (1984) first formally defended their monophyly.

NEMATISTIIDAE

Nematistius pectoralis Gill, USNM 82203, 153 mm.

Plate 147

Description.

LE1 on Eb1 uncinat process just lateral to cartilaginous tip.

LE2 on raised dorsoposterior edge of Eb2 about one-third length Eb2 laterally.

LE3 on medial edge of cartilaginous tip of Eb3 uncinat process.

LE4 broadly on Eb4 posterior surface lateral to uncinat process.

LP on Eb4 posterior surface beginning a little anterior to medial end of LE4 insertion, and extending a little lateral to LE4 insertion. Right-side LP only (not illustrated) with slender strap of LP muscle passing across posterior surface of LE4 and inserting on Eb4 at mid-posterior point of LE4 insertion.

LI1 insertion ventral to TPb2, on dorsoanterior-most bony and cartilaginous surface of anterior end of Pb2.

LI2 on Pb3 dorsolaterally, extending posteriorly to margin of medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 kidney-shaped pad, deeply notched mid-anteriorly with posterior end of notch continuing as laterally offset raphe (one side only; raphe gives rise dorsally to CT covering muscles); attached anterolaterally to cartilaginous anteriormost end of Pb2 at junction with IAC, free edge of muscle from this point laterally giving rise to CT sheet covering muscles; ventrally, broadly confluent with TEb2. TEb2 ventral to TPb2 and dorsal to OD3–4 origin, extending out about one-third distance along dorsal surface of Eb2 to point anterior to LE2. TPb3-Eb3 on Pb3 dorsal surface along medial edge of LI2, and, passing dorsal to medial end of Eb4, inserts on dorsoposterior surface of medial end of Eb3; continuous dorsoposteriorly by slender diagonal muscle strap with slender SOD.

OD3–4 anteriorly on dorsomedial surface of Pb3, posteriorly on anterior surface of Eb3 uncinat pro-

cess and anterior surface and medial edge of Eb4 uncinat process.

OP dorsally, broadly on Eb4 posterior surface just ventral to LE4 and LP insertions, ventrally, broadly on Cb5 bony posterior surface beginning medial to cartilaginous posterior tip, posteriorly overlapping Ad5 attachment to Cb5. On right-side only, OP ventrally becomes CT, which attaches to Ad5 posterior surface dorsal to Cb5 (not illustrated).

Ad1–3 absent.

Ad4 dorsally on ventral surface of distal one-third of Eb4, partly overlapped posteriorly by lateral edge of OP, ventrally on Cb4 medial to Eb4-Cb4 joint.

Ad5 on distal fourth of dorsal surface of Cb5 anterior to OP and dorsoposterior surface of Cb4 just ventral to AC.

SOD present.

RDs well separated.

Additional remarks. SCL attached mid-dorsally to posteroventral tip of Bb3. TV4 free from Cb5s. Pb2 toothed. AC dorsoposteriorly on cartilaginous distal tip of Cb4. Pb4 and UP4 present. Eb4 levator process absent.

CARANGIDAE

Selar crumenophthalmus (Bloch), USNM 189251 (not measured).

Plate 148

Additional material. ② = *Scomberoides tol* (Cuvier), USNM 76607, 136 mm.

Description.

LE1 on base of Eb1 uncinat process anteriorly. ② On uncinat process dorsoanteriorly.

LE2 on tip of expanded bony dorsoposterior margin of Eb2. ② On prominent bony process arising from posterior margin of Eb2.

LE3 finely, tendinously on tip of Eb3 uncinat process anteriorly. ② Musculously on Eb3 uncinat process anteriorly, there meeting OD3–4.

LE4 on Eb4 dorsally just lateral to uncinat process. ② On Eb4 dorsally between uncinat and levator processes.

LP on Eb4 beginning at and anterior to LE4 insertion and extending ventrolaterally, completely covering broad levator process, with posterior fibers continuous with Ad4 dorsoposteriorly. ② Levator process relatively small, muscle not continuous with Ad4.

LI1 on Pb2 broadly dorsally, beginning anteriorly near articulation with IAC.

LI2 on Pb3 dorsolaterally opposite medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3-Eb4. TPb2 dorsal to TEb2, pad-like with shallow lateral folds, anterior half of muscle transversely con-

tinuous, with mid-longitudinal raphe, which expands broadly replacing the muscle medially with an area of thick CT; CT sheets arise from lateral edge of raphe and from thick CT and attach to skull; muscle attaches anterolaterally to Pb2 dorsoanterior process adjacent to IAC and mid-ventrally along raphe with CT of pharyngeal roof. TEb2 joins TPb2 ventrally along mid-longitudinal raphe, and attaches strongly anteromedially to Pb3 dorsoanterolaterally posterior to LI1 insertion, and laterally on Eb2 dorsoanterolateral to LE2 insertion (strong attachment of TEb2 to Pb3 is unusual in acanthomorphs). TPb2 and TEb2 not joined musculously with TPb3-Pb4-Eb3-Eb4. TPb3-Pb4-Eb3-Eb4 broad, with mid-longitudinal raphe on anterior half; muscle attaches to Pb3 dorsoposteriorly medial to medial end of Eb3, continues posteriorly and attaches along posteromedial edge of Eb3, dorsal surface of Pb4, and dorsomedial surface of Eb4. ② TEb2 destroyed before determining if it was attached to Pb3. TD posteriorly appears to comprise only TPb3-Eb3-Eb4; what appears to be in same position as Pb4 in other carangids, appears to be an elongate cartilaginous tip of Pb3 to which UP4 is attached dorsally.

OD3–4, OD3'. OD3–4 origin on Pb3 dorsoposteromedially, below TEb2 posteriorly; insertion on anterior surfaces of Eb3 and Eb4 uncinat processes; OD3' (not illustrated) splits off ventrally from OD3–4 about half-way between origin and uncinat processes and inserts on Eb3 dorsally ventral to OD3–4.

OP dorsally on Eb4 uncinat process posteriorly, ventrally broadly tendinously on Cb5 posterolaterally, joining Ad5 posteroventrally.

Ad1–3 absent, but ropy GFMs present on anterolateral surfaces of each Eb-Cb arch.

Ad4 dorsally on Eb4 posterolaterally, mostly lateral to OP, continuous with LP; ventrally broadly on Cb4 dorsoposteriorly medial to Eb4-Cb4 joint.

Ad5 dorsally on medial surface of AC4 and posterodistal end of Cb4, ventrally on Cb5 dorsally, joining tendinous ventral end of OP. ② Dorsally joining raphe with OP.

SOD slender.

RDs separated by space less than one RD diameter.

Additional remarks. SCL attached mid-dorsally to ventroposteriorly extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. AC4 present.

A moderately well-developed Eb4 flange is present. Flange is absent in ②, moderately well developed in *Carangoides crysos*, very well developed in *Trachinotus falcatus*, and weakly developed and scarcely noticeable in *Selene vomer* and *Decapterus macrostoma*.

RACHYCENTRIDAE

Rachycentron canadum (Linnaeus), USNM 341455, 113 mm.

Plate 149**Description.**

LE1 broadly on Eb1 uncinat process anteriorly ventral to cartilage tip.

LE2 on dorsally expanded bony posterior edge of Eb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 narrowly tendinously on Eb4 just medial to tip of levator process.

LP broadly on dorsal surface of Eb4 anterior to tip of levator process and anteroventral to LE4 insertion.

LI1 on Pb2 dorsoanteromedially.

LI2 on Pb3 dorsally medial to broad medial end of Eb3.

TD comprises TEb2 and TPb3-Pb4-Eb3 (on left side only, a flat, thin, laterally curving, semicircular strand of muscle dorsal to TEb2, arising anteriorly, represents vestigial TPb2). TEb2 very broad centrally, ventrally continuous along mid-longitudinal raphe with CT of pharyngeal roof, narrowing laterally and joining medial edge of LE2 insertion, continuing laterally and attaching to Eb2 dorsally anterior to LE2 insertion, posteriorly continuous by diagonal strand of muscle with TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 dorsolaterally attaching to dorsoposteromedial surface of Eb3, ventrolaterally attaching to dorsoposterolateral surface of Pb3 and dorsal surface of Pb4, continuous by diagonal strand of muscle with SOD.

OD3-4, OD3' originates broadly on Pb3 dorsally ventral to TEb2, branches ventrally just lateral to origin; dorsal branch (OD3-4) inserts on bony anterior surfaces just ventral to cartilage tips of Eb3 and Eb4 uncinat processes. OD3' branches off OD3-4 ventrally shortly after emerging posteriorly from below TEb2, and inserts on Eb3 dorsally ventroanterior to OD3-4 insertion on Eb3.

OP dorsally on Eb4 posteroventrally beginning near medial end and extending laterally to point medial to levator process, ventrally on Cb5 dorsolaterally, joining raphe with ventroposterior end of Ad5, medially continuous with SO.

Ad1-3 absent.

Ad4 broadly on Eb4 ventrally beginning medially below levator process and extending laterally to bony end of Eb4, ventrally broadly on Cb4 medial to Eb4-Cb4 joint, joining Ad5 attachment on Cb4.

Ad5 dorsally on Cb4 posterolaterally and adjacent AC4, ventrally on Cb5 dorsolaterally anterior to OP.

SOD present.

RDs separated by space less than diameter of one RD.

Additional remarks. SCL questionably free from Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC present. Pb2 toothed.

CORYPHAENIDAE

Coryphaena equiselis Linnaeus, USNM 158126, 118 mm.

Additional material. ② = *Coryphaena hippurus* Linnaeus, USNM 340988, 105 mm; damaged preparation.

Plate 150**Description.**

LE1 originating tendinously and joining tendinous origin and anterior margin of LE2; inserting very broadly on Eb1 dorsoposteriorly and bony dorsoanterior surface of long uncinat process.

LE2 on expanded posterior edge of Eb2; anterior edge of muscle tendinous, attaching to tip of Eb1 uncinat process as muscle extends anterodorsally; tendinous edge joining tendinous dorsal extension of LE1 ventral to origin. ② Not possible to tell if LE2 attached to Eb1 uncinat process.

Remark. Ligament (Plate 150C, not labelled) attaches tip of Eb1 uncinat process posteriorly to anterior edge of Eb2 near anterolateral end of TEb2.

LE3 tendinously on tip of Eb3 uncinat process.

LE4 on Eb4 just lateral to uncinat process.

LP on Eb4 beginning at ventrolateral edge of LE4 insertion, continuing laterally to anterior edge of notched cartilaginous distal end of Eb4, crossing notch, and ending on AC4 medial to distal end of Eb4 and dorsal to medial end of Cb4. See also OP.

LI1 on Pb2 dorsoanteriorly, beginning on anterior process that joins medial end of IAC.

LI2 on Pb3 dorsolaterally.

TD comprises TPb2, TEb2, TEb3 (or possibly TEb3-Eb4, see remarks). TPb2 circular, pad-like, centrally thin, thickened laterally, with mid-longitudinal raphe, completely covering and apparently completely continuous with central portion of TEb2 and almost completely continuous laterally with TEb2, tenuously attached by CT only to dorsal surface of Pb2 anteriormost tip (attachment easily broken, not illustrated); circular area overlain with thin, very tightly applied CT sheet (could not be removed without damaging muscle). TEb2 inserting on most of dorsoanterior surface of Eb2, narrowly, weakly continuous mid-posteriorly with mid-anterior end of TEb3. TEb3 triangular, apex anteriorly continuous with TEb2, inserts along Eb3 dorsal surface ventral to OD3-4 and posterior to OD3', posteriorly continuous by diagonal muscle strap with SOD. ② TPb2 deeply undercut laterally and separated from TEb2; TEb2 well separated and unconnected with TEb3; TEb3 strap-like, not triangular.

Remarks. Very weak CT fibers questionably arise from mid-lateral dorsal surface of TEb3 and narrowly attach to medial edge of cartilaginous tip of Eb4 uncinat process. The connection was destroyed on both

sides inadvertently and was so tenuous that we decided against identifying TEb3 as TEb3-Eb4. ② Condition precluded determination if Eb4 connection was present.

There is no "substantive" attachment of TD to Pb3. Weak, filmy CT attaches the ventral surface of the combined TPb2-medial TEb2 to a tough CT sheet covering the dorsal surface of Pb3 (OD3–4 originates on dorsolateral edge of sheet).

M. Pb3-Eb2 (not illustrated) small, possibly anomalous muscle ventral to TEb2, present on only one side; originating on Pb3 dorsoanteriorly, joining raphe there with OD3–4, and inserting on dorsomedialmost bony surface of Eb2. ② Not present.

OD3–4, OD3' on Pb3 dorsolaterally ventral to TEb2, branches ventrally just lateral to origin; dorsal branch (OD3–4) inserts on bony dorsoanterior surface of Eb3 uncinat process and bony dorsomedial edge of Eb4 uncinat process; ventral branch (OD3') inserts along most of Eb3 dorsal surface ventral to OD3–4 insertion.

OP on left side broadly on posteroventral surface of Eb4 beginning ventral to uncinat process and extending medially, dorsolaterally joining LP along fine line of CT, muscle narrows as it extends ventrally and inserts on dorsodistal end of Cb5 together with Ad5 insertion. Right side OP, possibly abnormal (illustrated reversed in rear view), differs in having two separated portions dorsally, junction with LP along line of CT more extensive, fusing dorsoposteriorly with Ad4 dorsal attachment to Eb4. ② Both sides with single OP similar to that of left side of *C. equiselis*.

Ad1–3 absent.

Ad4 on Eb4 ventrolaterally, ventrally on Cb4 anterior to Eb4-Cb4 joint, posterolaterally joining raphe with Ad5 near insertion on Cb4 (not visible in Pl. 150).

Ad5 ventrally broadly on dorsolateral surface of Cb5 and dorsally on posterodistal surfaces of Cb4 and AC4.

SOD present.

RDs separate.

Additional remarks. SCL absent. TV4 free from Cb5s. IAC broadest laterally. Pb4 and UP4 present. Pb2 toothed. Eb4 levator process absent. AC4 present attaching to posterodistal end of Eb4 medially and dorsoposterodistal end of Cb4 (autogenous on one side and completely fused on other in ②). Small ACs present on first and second arches, possibly derived from segmentation of distal ends of Eb1 and Eb2, rather than from distal ends of Cbs. ② No ACs on first and second arches.

Johnson (1984:497) hypothesized that Coryphaenidae, Rachycentridae, and Echeneidae form a monophyletic group with Echeneidae as the sister group to the other two families. The results of a cladistic analysis reported by O'Toole (2002:617) corroborated the

monophyly of the three families, but indicated Coryphaenidae as the sister group of the other two families.

ECHENEIDAE

Echeneis naucrates, USNM 202201, 2: 150, 175 mm SL; USNM 206662, 145 mm.

Additional material. ② = *Remora remora* (Linnaeus), USNM 181890, 82.7 mm.

Not illustrated

Description.

Remarks. ② Differs from *Echeneis* primarily in composition of TD and relationship of LI2 to OD3–4.

LE1 broadly on bony anterior surface of Eb1 uncinat process.

LE2 broadly, dorsally, on anterior surface of expanded posterior margin of Eb2 at about mid-length.

LE3 variable: on tip of Eb3 uncinat process anteriorly or on joined tips of Eb3 and Eb4 uncinat processes anteriorly. ② Same variation (each side different).

LE4 and/or LP. See following remarks.

Remarks. Whether the relatively well-developed muscle inserting broadly on the flat bony surface of Eb4 well lateral to the uncinat process represents only LP or also includes LE4 is unclear (the muscle was destroyed during dissection of *Remora*). The muscle originates well posterior to the origins of the other levators, which originate near each other or together. This probably indicates that the muscle in question represents LP and that LE4 is absent, which is rare among acanthomorph fishes (also probably true of *Pholidichthys* and *Spinachia*). The gill-arches of echeneids are greatly appressed against the ventral skull surface and the origin of LE4 (if the muscle includes that levator) may have been separated posteriorly from those of the other levators with which it is normally associated. Additionally, the muscle on each side of each of the three specimens appears to incorporate two incompletely separated parts. We conclude parsimoniously that LP is present, and that LE4 is questionably absent. ② Information unavailable.

LI1 on dorsoanterior surfaces of Pb2 and adjacent Pb3; insertion is ventral to tough CT extending anteriorly from, and forming broad mid-section of TEb2.

LI2 largest levator, penetrating OD3–4 on way from origin to insertion on Pb3 broadly posterolaterally. ② Does not penetrate OD3–4, but passes ventral to it, as is usual in most acanthomorphs.

TD comprises TEb2, TEb3, and TUP4. TEb2 a broad muscle on each side joined by broad median area of tough CT covering large, muscously naked dorsal Pb3 facets; muscle forms anterior two-thirds

of lateral CT margin and attaches laterally in two separate areas on Eb2: on medial edge of bony process supporting LE2 and dorsally anterior to LE2 insertion. TEb3 a slender muscle on each side extending along posterior one-third of median area of tough CT covering Pb3 dorsal facets; muscle attaches on Eb3 dorsally medial to bony support of uncinate process. TEb3 continuous posteriorly by slender, diagonal muscle strand with broad, transversely musculously uninterrupted TUP4, which attaches to UP4 dorsally posterior to Pb4; posterolateral corner of muscle meets SO dorsolaterally and is broadly continuous posteriorly with SOD. ② Comprises TEb2 and TUP4-Eb4. TEb2 relatively slender, forms about one-fourth to one-third of lateral CT margin. TUP4-Eb4 transversely musculously continuous, attaching narrowly anterolaterally on Eb4 dorsomedially and on medial edge of UP4.

OD3–4 robust, origin broadly on lateral surface of musculously naked Pb3 dorsal facet, insertion on bony anterior surface and medial edge of Eb3 uncinate process and bony medial edge of Eb4 uncinate process; muscle penetrated by LI2, separating most of portion inserting on Eb3 from most of portion inserting on Eb4; posterolaterally, muscle forms raphe with OP dorsally. ② Muscle relatively flat, not penetrated by LI2, inserting on medial bony edges of Eb3 and Eb4 uncinate processes.

OP with two separate sections; dorsally medial section on posterior bony surface of Eb4 uncinate process, lateral section on posterior surface of levator process; two sections meet in raphe ventrally and attach on Cb5 posteromedially, posteromedial to medial end of Ad5; dorsally, OP sections overlap much of Ad4 posteriorly.

Ad1–3 absent.

Ad4 dorsally on Eb4 beginning posteroventrally and posterolaterally; medially mostly anterior to OP, extending laterally to end of Eb4 bony surface; ventrally on Cb4 anterior to both Ad5 and OP.

Ad5 dorsally on AC4 and distal end of Cb4 posteriorly, ventrally on Cb5 beginning dorsodistally and extending medially anterior to OP.

SOD present.

RDs moderately slender, separated by distance greater than one RD diameter.

Additional remarks. SCL present, but highly modified; apparently forming circle, the anterior portion of which is a sheet of tough ligamentous tissue. TV4 free from Cb5s. Pb4 and UP4 present. AC4 present. IAC absent.

Scombroidei

Johnson (1986) included the Sphyraenidae in the Scombroidei; however, Orrell et al. (2003:45 and in preparation) concluded based on a molecular study

involving outgroups and representatives of most putative scombroid genera that “there is no support for a close relationship between barracudas (Sphyraenidae) and the Scombroidei.”

POMATOMIDAE

Pomatomus saltatrix (Linnaeus), USNM 289926, 3 specimens, 113–126 mm.

Plate 151

Description.

LE1 on Eb1 uncinate process dorsoanteriorly ventral to cartilage tip.

LE2 on raised bony dorsoposterior edge of Eb2.

Remarks. In a large articulated gill-arch skeleton of *Pomatomus* (USNM 016528, specimen size unknown; gill arches 200 mm from basihyal to 5th Cb), a distinct, bony, prong-like process arises from Eb2 dorsoposteriorly.

LE3 on tip of Eb3 uncinate process dorsoanteriorly.

LE4 on dorsal edge of Eb4 levator process lateral to uncinate process, posteroventromedially joining raphe with OP dorsally.

Remarks. The cartilaginous portion of the Eb4 levator process varies in and among the three specimens: small, round cartilage, two separated small cartilages, or a single linear cartilage, all on the posterior edge of Eb4. The cartilaginous portion(s) is well lateral to the uncinate process and medial to the distal cartilaginous end of Eb4. These minute levator processes persist in large specimens, as indicated by remnants of their presence in a large skeleton (see remarks following LE2).

LP at and anterior to LE4 insertion.

LI1 on Pb2 dorsoanteriorly beginning posterior to IAC attachment to Pb2.

LI2 on Pb3 dorsolaterally well anterior to articulation with medial end of Eb3 and at and lateral to attachment of TPb3-Eb3 to Pb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2 squarish, dorsal to TEb2, with mid-longitudinal raphe, continuing posteriorly across TEb2; muscle attached anteroventrolaterally to dorsal end of Pb2 and adjacent dorsomedialmost surface of IAC, fusing ventroposteromedially with TEb2. TEb2 attaching laterally on dorsal surface of Eb2 at point anterior to ventromedial edge of LE2 insertion, posteriorly free and well separated from TPb3-Eb3. TPb3-Eb3 on Pb3 dorsoposteriorly beginning at and medial to LI2 and continuing onto dorsomedialmost surface of Eb3, continuous posteriorly by crossing muscle straps with SOD.

M. Pb3-Eb2 (not illustrated, easily overlooked.) small, hidden muscle originating on Pb3 at and anterior to LI2 insertion and inserting on Eb2 ventral to LE2 insertion.

OD3–4, OD3' origin ventral to TPb2 on dorsoanterior surface of Pb3, insertion on Eb3 uncinat process dorsoanteriorly and on medial edge and dorsoanterior surface of Eb4 medial to uncinat process. OD3' splits off ventromedial surface of OD3–4 shortly posterior to origin and inserts on Eb3 dorsally anteroventral to uncinat process.

OP dorsally on medial half of posterior surface of Eb4, joining raphe with LP posteroventromedially, ventrally on Cb5 dorsolaterally posterior to Ad5, joining raphe with Ad5 posterolaterally.

Ad1–3 absent.

Ad4, dorsally on posterolateral surface of Eb4, overlapped posteromedially by OP, ventrally on Cb4 medial to Eb4–Cb4 joint.

Ad5 ventrally on Cb5 dorsally mostly anterior to OP, dorsally on posterodistalmost surface of Cb4.

SOD present.

RDs adjacent or separated by space less than one-fourth diameter of one RD.

Additional remarks. SCL attached mid-posteriorly to ventroposterior cartilaginous distal end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb1 with dorsal and ventral cartilage ends. Pb2 toothed. PCI attaches to Cb5 beginning well medial to distal end and extends medially.

SCOMBROLABRACIDAE

Scombrolabrax heterolepis Roule, USNM 187651, 2 specimens, 98.5–104 mm.

Plate 152

Description.

Remarks. LE1 origin tendinous, all other levators originate musculously.

LE1 on dorsoposterior edge of Eb1 just lateral to tip of uncinat process.

LE2 on mid-dorsoposterior edge of Eb2.

LE3 on dorsomedial edge of tip of Eb3 uncinat process.

LE4 on dorsal edge of Eb4 between tips of uncinat and levator processes.

LP at and lateral to LE4 insertion, ventrolateral edge continuous with CT sheet attaching along edges of fourth and fifth arches and containing PP, which impinges on LP insertion.

LI1 on bony surface of Pb2 just ventral to joint with IAC.

LI2 on bony Pb3 dorsal surface lateral to TPb3–Eb3 attachment and anterior to medialmost end of Eb3.

TD comprises TPb2, TEb2, and TPb3–Eb3. TPb2 completely overlying TEb2 medially, almost circular, notched anteriorly with mid-longitudinal raphe, which attaches dorsally to CT sheets; muscle attached mid-anteriorly to CT of pharyngeal roof, attachment continuing dorsolaterally to (and over) dorsoanterior

end of Pb2, at which point flat laterally convex ribbon of muscle arises (on each side) and continues to posterior end of mid-longitudinal raphe; ventral surface fused with TEb2, but muscle partially replaced by CT on mid-portion of right side (TEb2 visible through CT); TPb2 strongly attached to Pb2, overlies anterior end of Pb3 to which it is loosely attached. TEb2 extending laterally on dorsoanterior surface of Eb2 anterior to LE2 insertion, well separated from, but connected mid-posteriorly by CT (not illustrated) to TPb3–Eb3. TPb3–Eb3 anteriorly broadly on Pb3 dorsal surface medial to LI2 insertion, posteriorly narrowly on posteromedial surface of Eb3, continuous posteriorly by transverse muscle strands with SOD.

OD3–4 originating on dorsoanteromedial edge of Pb3 ventral to TEb2 and inserting on joined anterior surface of Eb3 uncinat process and medial edge of Eb4 uncinat process.

OP dorsally broadly on posterior surface of medial arm of Eb4 beginning just lateral to levator process and extending medially to end of bony surface, mid-medially inseparable from SO, ventrally broadly on dorsoposterior edge of Cb5 mostly posterior to Ad5.

Ad1–3 absent.

Ad4 broadly dorsally on Eb4 dorsoposterior surface beginning below levator process and extending laterally to bony distal end, ventrally narrowly on Cb4 medial to Eb4–Cb4 joint.

Ad5 broadly on Cb5 dorsolaterally, mostly antero-medial to OP, very narrowly on posterodistalmost end of Cb4.

SOD present.

RDs slightly separated.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. PCI attaches on Cb5 beginning medial to distal end and continues medially; origin is from cleithrum by long tendon.

SCOMBRIDAE

Scomber scombrus Linnaeus, USNM 203841, 143 mm.

Plate 153

Description.

LE1 very short, on tip of Eb1 uncinat process, insertion tendinous.

LE2 inserts by long tendon on dorsomedialmost edge of long bony Eb2 process.

LE3 inserts by long tendon on dorsomedialmost edge of cartilaginous tip of Eb3 uncinat process, muscle becomes tendinous dorsally and then muscular again before attaching to skull.

LE4 inserts by long tendon on posterodorsal edge of Eb4 lateral to uncinat process.

LP absent.

LI1 tendinously on Pb2 dorsally slightly anterior to joint with medial end of Eb2, joining raphe anteromedially with anterolateral side of TPb2, where anteromedial edge of TEb2 meets TPb2; about same size as LI2.

LI2 on Pb3 dorsoposterolaterally.

TD comprises TPb2, TEb2, TPb3-Eb3. TPb2 thin, oval, attached dorsomid-longitudinally to thin, tough CT sheet, mid-anterioventrally to CT of pharyngeal roof, and anteroventrolaterally to broad cartilaginous end of Pb2 just medial to articulation with IAC, continuous ventrally with TEb2 (only narrow, arcing, free lateral edge distinguishes TPb2 from TEb2). TEb2 on Eb2 dorsally medial to LE2 insertion on long bony process and just anterior to anterior attachment of GFM2. TPb3-Eb3 broadly on Pb3 bony surface beginning anteriorly at about mid-length of bone and well medial to lateral margin and LI2 insertion, continuous posteriorly by thin diagonal muscle strands with Eb3 portion, which is on postero-medial surface of Eb3.

M. Pb2-Eb1 (not visible in dorsal view) on Pb2 anterolaterally ventral to joint with IAC, and on Eb1 posterior surface ventral to uncinat process.

Remarks. M. Pb2-Eb1 occurs otherwise only in pre-acanthomorphs.

OD3–4, OD3' origin on most of dorsoanteromedial surface of Pb3 ventral to TEb2, dividing posteroventrally, with short ventral branch (OD3') inserting on dorsomedial surface of Eb3 and combined dorsal insertion on medial surface of Eb3 uncinat process ventral to cartilage tip and bony dorsomedial edge of Eb4 uncinat process.

OP dorsally on Eb4 posteriorly beginning medially at point between medial end and uncinat process and extending laterally well past uncinat process, to below LE4 insertion, ventrally on Cb5 joining tendon (raphe) with posterior edge of Ad5.

Ad1–3 absent. GFM1 and GFM2 present, superficially appear to be RecD2 and RecD3, but are associated with gill filaments. Not interpreted as Ad1 and Ad3, because they do not extend onto associated Cbs. GFM2 on anterior edge of Eb2 anterior to prominent bony process supporting LE2, narrowing to point at attachment to ventrolateral edge of bony process supporting cartilage tip of Eb1 uncinat process, lateral edge of muscle associated with gill filaments. GFM3 on dorsolateral edge of prominent Eb2 process and anterior edge of Eb3 mid-laterally, lateral edge of muscle associated with gill filaments.

Ad4 on ventral surface of Eb4 dorsolaterally and dorsodistal surface of Cb4 anterior to Eb4-Cb4 joint, ventroposteriorly fusing with Ad5 on Cb4.

Ad5 moderately broadly on dorsodistal margin of Cb5 and narrowly on AC4 and posterodistalmost end of Cb4, fusing at about mid-anterior surface with Ad4 and ventrally joining tendinous edge of OP.

SOD present.

RDs separated by distance greater than twice diameter of one RD, each with small separate branch.

Additional remarks. SCL present attached mid-dorsally to cartilaginous ventroposterior tip of Bb3. TV4 free from Cb5s. Pb4 absent, UP4 present. Eb4 levator process absent. AC4 attached to posterodistal end of Eb4 and dorsodistal end of Cb4 (also present in *Rastralliger kanagurta* (Cuvier), USNM 192526; not present in *Scomberomorus cavalla* (Cuvier), USNM 289928, which has a similarly positioned AC between Eb3 and Cb3). PCI attaches on Cb5 well medial to distal end and continues medially.

Two enlarged, modified gill-raker patches are present on each side of SO (seen in posterior view, Pl. 153B); internally these patches support filamentous teeth. Similarly positioned gill-raker patch noted in present study only in Melamphaidae.

Sparoidei

Orrell et al. (2002), based on a molecular phylogenetic study, provided evidence that Lethrinidae are the sister group of the Sparidae, within a weakly supported monophyletic group comprising Sparidae, Centranchidae, Lethrinidae, and Nemipteridae. Carpenter and Johnson (2002), in a morphological phylogenetic study (not involving muscles), however, hypothesized Nemipteridae (Lethrinidae (polytomus Sparidae-Centranchidae)). In another molecular phylogenetic study, Orrell and Carpenter (2004) found that Sparidae are monophyletic only with inclusion of Centranchidae, which was not monophyletic. In the same study, Sparoidei was not monophyletic with inclusion of either Nemipteridae or Lethrinidae, nor did the latter two families form a monophyletic group.

NEMIPTERIDAE

Nemipterus furcosus (Valenciennes), USNM 349457, 2 specimens, 93.5–104 mm.

Plate 154

Description.

LE1 on tip of bony uncinat process at mid-length of Eb1. Cartilage tipped Eb1 uncinat process absent.

LE2 on raised posterior edge of Eb2; insertion posteroventrally continuous with ligament attaching Eb2 to Eb3 anteriorly.

Remarks. Imamura (2000:214) described LE2 in nemipterids as inserting on both Eb2 and Eb3, a condition he found limited otherwise among percormorphs to malacanthids. We believe the state in malacanthids is different from that in nemipterids; see remarks following description of LE2 in Malacanthidae. The nemipterid condition is more common than Imamura recognized, although we did not always note it in our descriptions.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 levator process anteriorly.

LP on Eb4 beginning at LE4 insertion posterolaterally and extending laterally.

LI1 on dorsoanteriormost surface of Pb2 beginning dorsally just ventral to cartilage tip.

LI2 on Pb3 dorsolaterally just anterior to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb4-Eb3. TPb2 a pair of muscles, each laterally convex, joined to each other posteromedially and to TEb2 ventroposteromedially; TPb2 and TEb2 attach to dorsalmost tip of Pb2 posteriorly. TEb2 attaches mid-anteroventrally to CT of pharyngeal roof, with mid-longitudinal raphe, which gives rise dorsally to CT sheets covering muscles; TEb2 attaches laterally on Eb2 surface lateral to LE2 insertion; muscle not continuous posteriorly with TPb4-Eb3. TPb4-Eb3 anteriorly ventral to TEb2, continuous posteriorly with longitudinal SO muscle that extends anteriorly between Pb3s; TPb4-Eb3 dorsally slender, winglike, attaching to Eb3 posterior edge medial to uncinat process, ventromedially attaching to Pb4 dorsally, continuous posteriorly with SOD.

Remarks. Attachment of TEb2 to Pb2 is uncommon; also present, homoplastically, in *Amarsipus* (Amarsipidae).

CPb (not illustrated) moderately well-developed, extending along lateral surfaces of Pb2, Pb3 and UP4 and attaching to lateral ends of Pb2 and UP4, with weak anterior branch extending medially between Pb2 and Pb3 and posterior branch between Pb3 and UP4, anterior branch joining even weaker muscle attaching to Pb2 posteromedially and, together with posterior branch, fading into sparse SO muscle fibers of pharyngeal roof. In the smaller specimen, CPb does not extend anteriorly past its attachment to Pb2; in the larger specimen, muscle continues anteriorly from the attachment and begins to attenuate greatly at about the mid-anterior Pb2 margin, then fades into SO fibers medially.

OD3, OD3', OD4 all well developed, originating massively and essentially together from a dorsomedially raised bony flange on Pb3 and the Pb3 surface ventrolateral to it, and separating almost immediately into OD3 and OD4 dorsally and longitudinally, and OD3' ventrally from the other two. OD3 inserts on Eb3 uncinat process anteriorly, OD3' on Eb3 dorsally ventral to uncinat process, and OD4 on Eb4 levator process (uncinat process absent).

OP dorsally on Eb4 posteriorly medial to levator process and ventrally on Cb5 posterolaterally, joining small raphe at its ventrolateralmost edge with Ad5 ventroposteriorly.

Ad1-3 absent.

Ad4 dorsally on Eb4 posteriorly beginning anterior to OP and extending laterally and attaching to Eb4

ventrally near joint with Cb4, ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally, moderately broadly on Cb4 postero-laterally, ventrally less broadly on Cb5 dorsolateral to OP.

SOD broad.

RDs separated by space less than half one RD diameter.

Additional remarks. SCL very fine, easily broken, attached mid-dorsally to cartilaginous ventroposterior tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC absent. Pb2 toothed.

Eb4 uncinat process absent, as inferred from insertion of LE4 on levator process (in acanthomorphs, LE4 inserts on the uncinat only in a few basal taxa, e.g., *Lampris*, *Velifer*. Also, indicated by apparent reduction in size of the uncinat process and juxtaposition of it near the levator process in the closely related *Lethrinus* (Lethrinidae, q.v.). Carpenter and Johnson (2003:120) report that the absence of the Eb4 uncinat process is apomorphic for the Nemipteridae among the sparoids.

Cartilaginous, meniscus-like pad (not illustrated) present, tightly and closely attached and conforming with dorsal surface of ventral cartilaginous end of Pb1. Pad is easily overlooked, but appears to act as cushion between skull and Pb1, which curves around skull and attaches dorsally to it.

Carpenter and Johnson (2002) hypothesized the monophyly of the Sparoidea, in which they included nemipterids as the sister group to lethrinids, and these together as the sister group of sparids and centrarchids.

LETHRINIDAE

Lethrinus obsoletus (Forsskål), USNM 309317, 2 specimens, 84.3-103 mm.

Plate 155

Additional material. ① *Lethrinus harak* (Forsskål), USNM 259390, 85.5 mm. ② = *Gymnocranius griseus* (Temminck and Schlegel), 350957, 115 mm. ③ = *Monotaxis grandoculis* (Valenciennes), USNM 264135, not measured.

Description.

LE1 broad based, on Eb1 just lateral to tip of uncinat process; origin long, tendinous.

LE2 on dorsally expanded posterior margin of Eb2.

LE3 finely tendinously on tip of Eb3 uncinat process anteriorly.

LE4 on tips of Eb4 levator and uncinat processes (see Additional remarks).

LP finely, tendinously on Eb4 lateral to and not coincident with LE4 insertion (see Additional re-

marks). ② ③ LP insertion joins LE4 insertion laterally.

LI1 on Pb2 dorsolaterally beginning ventral to TPb2 attachment to Pb2 and extending ventrally.

LI2 on Pb3 dorsoanterolaterally just posterior to Pb2 posterolaterally.

TD comprises TPb2, TEb2, and TPb3-Eb4. TPb2 thick, laterally convex muscle pair lying dorsal to TEb2 and joined posteriorly by CT, which extends anteriorly as mid-longitudinal raphe of TEb2, which gives rise dorsally to CT sheets covering muscles and attaching to skull; anteriorly each member of TPb2 pair attaches to Pb2 dorsoanteriorly; posteromedially, along extension of raphe, and just anterior to its posterior end, each TPb2 member is joined ventrally by TEb2, which is transversely continuous anteriorly. Anterolaterally on each side, TEb2 joins TPb2 at attachment to Pb2; laterally TEb2 attaches on Eb2 dorsally lateral to LE2 insertion; lateral end of TEb2 divides into anterior and posterior branches, with medial end of fine Ad2 inserting into divide (not apparent on Plate 155A); TEb2 attached mid-ventroanteriorly between Pb3s to CT of pharyngeal roof; muscle not continuous posteriorly with TPb3-Eb4. TPb3-Eb4 ventral to origin of OD3-4 and OD3', begins on Pb3 dorsolaterally just medial to posteromedialmost edge of Eb3 and is dorsomedially continuous with Eb4 portion of muscle anteroventrally; Eb4 portion is mostly separate from Pb3 section, and inserts on dorsomedial bony surface of Eb4; Pb3 portion is ventromedially continuous with SOD, which is completely obscured in dorsal view of gill arches. ② TD includes TPb3-Eb3-Eb4 instead of TPb3-Eb4; only few strands of muscle attach to posteromedial surface of Eb3. ③ TD includes TPb3-Pb4-Eb3 instead of TPb3-Eb4; only few strands of muscle attach to dorsomedial surface of Pb4.

CPb very prominent externally, especially anteriorly, where it is transversely continuous; completely encircles Pb2 and Pb3 and attaches to posterolateral and posteromedial corners of UP4; medial fibers pass into SO longitudinal fibers. ③ Muscle extends only from mid-lateral surface of UP4 on one side anteriorly around to mid-lateral surface of UP4 on other side.

OD3-4, OD3' origin broadly on Pb3 dorsomedially; OD3-4 insertion on entire anterior surface of Eb3 uncinat process and entire medial edge of Eb4 leading to levator and uncinat processes; OD3' splitting off from OD3-4 almost immediately distal to origin and inserting on Eb3 dorsal surface ventral to Eb4 insertion of OD3-4.

OP dorsally on most of bony posterior surface of Eb4 medial to levator process, ventrally broadly on Cb5 posteriorly, ventrally joining raphe with PCI (see Additional remarks).

Ad1-3 relatively weak, on anterior surfaces of rel-

evant Eb and Cb; Ad2 extending medially onto dorsal surface of Eb2 between split lateral end of TEb2.

Ad4 dorsally broadly on Eb4 posteriorly beginning medially on levator process and extending almost to lateral end of bone; ventrally broadly on Cb5 posteriorly.

Ad5 dorsally relatively narrowly on Cb4 posterolaterally and ventrally on Cb5 dorsolaterally.

SOD present, ventral to TPb3-Eb4, not visible in dorsal view in illustrated specimen, but posterior to TPb3-Eb4 and visible in dorsal view in other specimen and taxa.

RDs adjacent.

Additional remarks. SCL absent (but Bb3 has a very elongate posteroventrally extending cartilaginous end, normally present when SCL is present). TV4 free from Cb5s. IAC present. Pb1 bony with cartilage tips. Pb2 toothed. Pb4 and UP4 present.

Displacement of LP insertion from joining or meeting LE4 insertion appears to be unique to *Lethrinus* among acanthomorphs.

In lethrinids, the uncinat processes on Eb3 and Eb4 are not bound together as they are in most acanthomorphs. The bony support of the Eb4 uncinat process is indistinguishable from that of the levator process and its cartilaginous tip, when present, is greatly reduced (vestigial) and barely separated from that of the levator process. In the nemipterids, the uncinat process has been entirely lost. The association of LE4 with the tip of Eb4 uncinat process is not the same condition as occurs in *Caristi* (*Caristiidae*) in which the uncinat process is well developed and in its usual position (joining Eb3 uncinat process) and there is no Eb4 levator process.

PCI inserts broadly on Cb5 reaching the cartilage tip of the element in *Gymnocranius* and *Monotaxis*, failing to extend even near the tip in both species of *Lethrinus*. OP joins raphe with PCI.

CENTRACANTHIDAE

Spicara smar (Linnaeus), USNM 269800, 2 specimens, 86.0-90.6 mm.

Plate 156

SPARIDAE

② = *Acanthopagrus bifasciatus* (Forsskål), USNM 191682, 71.8 mm.

Additional material. ③ = *Lagodon rhomboides* (Linnaeus), USNM 143843, not measured. ④ = *Sarpa salpa* (Linnaeus), USNM 343618, 73.6 mm.

Not illustrated

Remarks. Carpenter and Johnson (2002) hypothesized that centracanthids and sparids form a monophyletic group "with placement of centracanthids unresolved with respect to sparid genera [p. 114]"

among the Sparoidea, which also includes nemipterids and lethrinids.

Except for CPb, muscles for all three sparid taxa we include were recorded only as present or absent, and all are present as in *Spicara*, although the finer details of the descriptions for *Spicara* may not apply to the sparid taxa.

Description.

LE1 on dorsoanterior surface of bony Eb1 uncinate process.

Remarks. The medial edge of the tip of the uncinate process is minutely cartilaginous and easily overlooked.

LE2 narrowly tendinously on raised posterior edge of Eb2 anteriorly.

LE3 finely tendinously on tip of Eb3 uncinate process anteriorly.

LE4 finely tendinously on tip of Eb4 levator process anteriorly.

LP on dorsal surface of Eb4 lateral to levator process.

LI1 on Pb2 dorsally at base of cartilage-tipped dorsal process that articulates with IAC.

LI2 on Pb3 dorsolaterally medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 pair of flat, laterally curving muscles dorsal to TEb2; each member of pair attaching anteriorly to Pb2 cartilage-tipped anterior process; pair joined posteromedially by raphe, which continues anteriorly along center of TEb2; dorsally, raphe gives rise to CT sheets covering muscles and attaching to skull; TPb2s join TEb2 at raphe, which is attached ventrally to CT of pharyngeal roof between Pb3s; TPb2 and TEb2 not continuous posteriorly with TPb3-Pb4-Eb3. TEb2 broad, extending laterally and attaching to Eb2 dorsally anterolateral to LE2 insertion, meeting medial end of Ad2, failing to cover dorsoposterior Pb3 surfaces in illustrated specimen (probably unusual), but does so in other specimen and three sparid genera examined. CPb. TPb3-Pb4-Eb3 on Pb3 dorsoposterolaterally at medial end of Eb3, continuing posteriorly on small Pb4 dorsally, and extending well laterally and attaching finely on posterior bony edge of Eb3 medial to uncinate process and posterior to OD3'; TPb3-Pb4-Eb3 continuous posteroventrally by crossing strands of muscle with SOD.

CPb (not illustrated) relatively weak muscle strands beginning on posterolateral corner of UP4, continuing anteriorly along Pb3 laterally and attaching to posterolateral end of autogenous tooth plate (Pb2'; see also remarks) joined to Pb2 posteriorly and absent from Pb2' laterally, but beginning again on Pb2' anterolaterally and continuing anteriorly around Pb2 and across mid-line of arches to opposite side; muscle strands from posterior end of Pb2' also pass

medially between Pb2 and Pb3, with short branch attaching to Pb2 posteromedially and longer branch continuing posteriorly along medial side of Pb3 and attaching to posteromedial side of UP4, with strands also passing laterally between Pb3 and UP4 and joining strands passing anterolaterally to UP4 and Pb3. Muscle absent on Pb2 laterally, Pb2' mid-laterally, and UP4 posteriorly.

Remarks. CPb present in ② and ③, in which strands may be continuous anteriorly along Pb2' laterally, but absent in ④.

Pb2', which articulates closely with the posterior end of Pb2, has been treated as an Eb2 tooth plate (e.g., Carpenter and Johnson, 2002:120, character no. 34; see also discussion by Johnson (1992:19, item 4)) and is arbitrarily treated here as a part of Pb2.

OD3–4, OD3' origin broadly on Pb3 dorsally, anteriorly ventral to TEb2; muscle dividing ventroanterolaterally well lateral to origin, with separate ventral insertion (OD3') on Eb3 dorsally ventroanterior to uncinate process, meeting medial end of Ad3, and (OD3–4) on Eb3 uncinate process anteriorly and Eb4 uncinate and levator processes medially.

OP dorsally on Eb4 posteriorly medial to levator process, ventrally on Cb5 dorsoposteriorly, laterally joining raphe with Ad5 medially.

M. Pb3-Cb5 diagonal strap of muscle attaching to Pb3 posteriorly and extending posteriorly medial to medial end of Eb4, then ventrally and attaching tendinously to posterodistal surface of Cb5.

Remarks. Muscle appears restricted to centrarchids and sparids and provides additional evidence of the close relationship of these two groups.

Ad1–3, short, each on anterodistal surfaces of relevant Eb and associated Cb.

Ad4 dorsally on Eb4 posteriorly beginning on levator process and extending laterally, ventrally on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 anteriorly on posterodistal surface of Cb4 and posteriorly on Cb5 dorsally, joining raphe dorsomedially with OP ventrolaterally.

SOD present.

RDs separated by space about one-half diameter one RD.

Additional remarks. SCL present (also ④). ② ③ Attached mid-dorsally to tip of ventroposteriorly curving cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present.

Carpenter and Johnson (2002) described the peculiar relationship of Pb1 to Eb1 in centrarchids. The cartilaginous ventral end of Pb1 tightly joins and conforms with the dorsomedial surface of the anterior arm of Eb1, whereas the two elements are loosely articulated in the sparids, lethrinids and nemipterids. Additionally, we found that Pb1 of centrarchids appears to have pivoted laterally from its articulation with Eb1 and that it is the ventrolateral surface of

the cartilaginous ventral end that is joining Eb1. Also, there is a thin wafer of fibrocartilage (not illustrated in Plate 156) that is tightly joined to the dorsal surface (or dorsomedial surface if Pb1 were upright) of the cartilaginous ventral end of Pb1. The wafer rests against the ventral surface of the cranium and probably serves as a cushion.

Girelloidei

Girelloidei here coined as a subordinal taxon to facilitate designating a group of families (Girellidae, Scorpidae, Microcanthidae, Kyphosidae, Kuhliidae, Terapontidae, Arripidae, Oplegnathidae, but excluding those belonging to the Stromateoidei) that Johnson and Fritsche (1989) hypothesized formed a monophyletic group. The group, including stromateoids, was based primarily on their possessing Freyhof's (1963) pattern 10 of the ramus lateralis accessorius (RLA). Johnson and Fritsche did not examine *Amarsipus*, sole member of the Amarsipidae, which has been included as a stromateoid since its original description (Haedrich, 1969). *Amarsipus* lacks the striking complex specialization that characterizes all other stromateoids (see both *Amarsipus* and *Icosteus*, Icosteidae, for discussions of the inter-relationships of *Amarsipus*), and if it is a stromateoid, is most probably the sister group of all other stromateoids. We examined *Amarsipus* for the presence of pattern 10 of RLA, and found it absent, but are uncertain which of the other patterns it possesses. *Amarsipus*'s relationship with other stromateoids is, therefore, an open question.

We only examined the musculature of three of the families of Girelloidei, and noted no information bearing on its monophyly.

GIRELLIDAE

Girella simplicidens Osburn and Nichols, USNM 167579, 95.6 mm, USNM 321278, 78.0 mm.

Not illustrated

Description.

LE1 on Eb1 posteriorly at about mid-length and well lateral to tip of horizontally directed uncinat process; tendon runs along lateral surface of muscle.

LE2 on Eb2 posteriorly at about mid-length; slender tendon runs along ventral half of lateral edge of muscle.

LE3 on tip of Eb3 uncinat process medially.

LE4 on Eb4 posteriorly projecting levator process dorsally.

LP on Eb4 dorsally a little lateral to LE4 insertion.

Remarks. Among percomorphs, only *Girella*, *Rachycentron* (Rachycentridae), *Spicara* (Centracanthidae), lethrinids, and several atherinomorphs have LP inserting completely separate from LE4. In other per-

comorphs, the two muscles almost always insert together and the insertions are often fused.

LI1 on Pb2 dorsally just posterior to anteriormost tip; about same size as LI2.

LI2 finely, tendinously on Pb3 dorsally immediately medial to articulation with medial end of Eb3, near, if not bordering lateral edge of TPb3-Pb4-Eb3 on Pb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3 (TPb3-Pb4-Eb3-Eb4 in smaller specimen). TPb2 a thick, laterally curving, semicircular muscle on each side dorsal to TEb2 and ventral to thick CT pad; muscle arises posteriorly from posterolateral edge of moderately broad CT area, which narrows anteriorly into mid-longitudinal raphe as it extends across TEb2, gives rise to thick CT pad dorsally, and continues anteriorly with CT of pharyngeal roof; anteromedially muscle fades into TEb2; muscle impinges on Pb2 dorsoanteriorly, but is at most weakly, if at all attached to Pb2. TEb2 extends laterally onto Eb2 dorsally to point anterior to LE2 insertion, meeting medial end of GFM2. TPb3-Pb4-Eb3 beginning on Pb3 dorsolaterally a little anterior to articulation with Eb3, extending posteriorly and attaching to posterior corner of medial end of Eb3 and, not visible externally, ventrally attaching on dorsal surface Pb4 (and on dorsal surface of medial end of Eb4 in smaller specimen); muscle continuous posteroventrally by fine muscle strands (not visible externally) with SOD.

OD3-4 anteriorly on Pb3 dorsomedially ventral to TEb2, posteriorly on Eb3 broadly anteriorly beginning just ventral to tip of uncinat process and on Eb4 anteriorly beginning ventrolateral to uncinat process (muscle divides as it extends posterolateral from medial edge of Eb3 uncinat process).

OP dorsally on Eb4 ventrally, beginning a little lateral to medial end of Eb4 and extending laterally and curving posteriorly as it follows posteriorly projecting bony Eb4 shelf, but ending on shelf well anterior (medial) to its posterior cartilage tip (levator process); ventrally on Cb5 posteriorly, beginning medial to distal end and continuing medially a short distance past attachment of Ad5; lateral edge of muscle is tendinous, becoming fascia-like on attaching to Cb5 and joining dorsomedial edge of Ad5; medially muscle is indistinguishable from SO. When gill arches are viewed posteriorly, only OP dorsal and ventral portions are visible, as Ad4 occludes mid-portion from view.

Ad1-3 absent; moderately well-developed GFMs1-3.

Ad4 very broad, dorsally on Eb4 ventrally, beginning medially anterior to dorsolateral end of OP, extending laterally posterolaterally around posteriorly projecting Eb4 shelf (supporting levator process), then laterally to end of bony Eb4 surface; ventrally relatively narrowly on Cb4 dorsally medial to Ad5.

Ad4, other than SO, is main muscle visible in posterior view of gill arches.

Ad5 relatively small, anteriorly on posterodistal surface of Cb4 and Eb4 at joint and lateral to OP laterally, joining CT with OP ventrolaterally; posteriorly on Cb5 posterodistally.

SOD present.

RDs adjacent.

Additional remarks. SCL weakly attached mid-dorsally to ventrally projecting cartilaginous posterior end of Bb3. TV4 free from Cb5s. Pb1 present, mostly bony. Pb2 toothed. Pb4 and UP4 present. IAC present. Medial end of Eb4 larger than medial end of Eb3. Eb4 flange absent.

KUHLIIDAE

Kuhlia mugil (Forster), USNM 114998, 2 specimens, 87.0–94.8 mm.

Plate 157

Description.

LE1 on bony surface of Eb1 uncinat process beginning just lateral to joint with IAC.

LE2 on dorsalmost edge of raised dorsoposterior margin of Eb2.

LE3 on Eb3 extending laterally from medial edge of cartilage tip of uncinat process.

LE4 on Eb4 bony surface just medial to cartilage tip of levator process.

LP on Eb4 bony surface beginning just anterior to cartilage tip of levator process and extending to and joining LE4 insertion anteriorly.

LI1 insertion mainly on dorsoposteriormost edge of Pb2 anterior process, with CT attachments to IAC dorsoposteromedialmost surface (adjacent to Pb2 insertion) and anterolateralmost edge of TPb2.

LI2 on Pb3 dorsoposteriorly immediately medial to anteromedialmost edge of Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb3. TPb2 divided; medially concave cord-like muscle on each side dorsal to TEb2; attaches anteromedially to dorsoanteriormost end of Pb2 with membranous continuations onto IAC medially and adjacent LI1 insertion; anteromedially joining irregular mid-longitudinal raphe with TEb2 anteriorly, posteromedially fading into TEb2; CT sheets arising from irregular mid-longitudinal raphe attach also on surface of TPb2. TEb2 flat medially, with irregular mid-longitudinal raphe, which is continuous ventroanteriorly with CT of pharyngeal roof; muscle thickening laterally and attaching broadly dorsally on Eb2 anteroventral to LE2; muscle discontinuous with TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 attaching on Pb3 dorsolaterally ventral to OD3–4 and just medial to mid-medial edge of Eb3, continuing posteriorly on Eb3 posteromedial edge and ventrally on Pb4 dorsally (attachment on

Pb4 obscured in dorsal view), continuous by diagonal muscle strand with SOD.

OD3–4 origin broadly on Pb3 dorsoposteromedially ventral to TEb2, insertion broadly on Eb3 dorsoanteriorly beginning just ventral to tip of uncinat process and narrowly on medial edge of Eb4 just ventral to tip of uncinat process or on anterior surface just ventral to tip of uncinat process.

OP dorsally on Eb4 posteriorly beginning at medial end of bony surface and extending laterally to below, or slightly lateral to, uncinat process, ventrally joining tough, clear CT (not illustrated) surrounding Ad5, and attaching to Cb5 ventromedially continuous with SO.

Ad1–3 absent (GFM's moderately developed).

Ad4 dorsally on Eb4 posteriorly beginning slightly anteromedial to lateral edge of OP and extending laterally to below levator process, there becoming sharply less robust and extending somewhat ventrally to end of bony surface; ventrally, narrowly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 posterodistally and AC4 ventrally; ventrally on Cb5 posterolaterally. Muscle encased in tough, clear CT (removed in Plate 157), which is joined by OP ventrally.

SOD present in both specimens.

Johnson (1993:9) reported that SOD is absent in *Kuhlia* (see also remarks following SOD in *Toxotes* (Toxotidae) description).

RDs adjacent or very slightly separated.

Additional remarks. SCL attached mid-dorsally to ventroposteriorly extending cartilage tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. AC4 present (also in cleared and stained specimen of *K. sandvicensis* (Steindachner), USNM 289471).

TERAPONTIDAE

Leiopotherapon unicolor (Günther), USNM 173654, 96.3 mm; USNM 173858, 120 mm, cleared and stained gill arches.

Plate 158

Additional material. ② = *Terapon jarbua* (Forsskål), USNM 173657, 81.1 mm.

Description.

LE1 slender, on tip of Eb1 uncinat process; muscle and Pb1 attached anteriorly to pharyngeal roof CT. ② Not especially slender.

LE2 finely, tendinously on Eb2 mid-dorsoposteriorly. ② Insertion muscular, not fine.

LE3 on Eb3 uncinat process dorsoanteriorly just ventral to cartilage tip.

LE4 on Eb4 posteriorly projecting levator process; ventroposterolateral and ventroposteromedial fibers continuous with Ad4. ② LE4 and Ad4 not continuous.

LP on Eb4 beginning at ventro-anterolateral edge of LE4 insertion and continuing laterally a short distance; posterolateralmost fibers continuous with Ad4 dorsally. ② Fibers not continuous with Ad4.

LI1 on Pb2 dorsally just posterior to anteriormost tip. ② On Pb2 similarly, but, with additional attachment to posterior surface of Pb2-IAC joint.

LI2 on Pb3 dorsolaterally just medial to medial end of articulation with Eb3.

TD comprises TPb2, TEb2 and TPb3-Eb3. TPb2 a thick, irregularly round, concave pad dorsal to TEb2, with mid-posterior notch extending anteriorly as raphe, from which tough, filmy CT sheets arise and also attach to pad dorsolaterally; muscle attaches anterolaterally to Pb2 and fuses ventrally with mid-medial area of TEb2. TEb2 attaches by CT mid-ventrally to CT of pharyngeal roof, extends on Eb2 dorsally to medial surface of tiny, low, diagonal bony strut anterior to LE2 (medial end of GFM2 attaches to lateral surface of strut). TPb2 and TEb2 not continuous with TPb3-Eb3. TPb3-Eb3 on Pb3 posterolaterally beginning just anterior to LI2, continuing posteriorly medial to LI2 insertion and extending onto Eb3 posteromedially; muscle continuous posteriorly by diagonal muscle strand with SOD. ② Strut weakly developed, would have been overlooked without knowledge of occurrence in *Leiopotherapon*—development possibly related to size of specimen.

OD3–4, OD3' originate together on Pb3 medially ventral to TEb2 and TPb3-Eb3, extend laterally with short OD3' branch separating anteroventrally and inserting on Eb3 dorsally ventral to uncinate process, there meeting medial end of GFM3. Major portion of muscle continues laterally with anterior portion inserting broadly on Eb3 uncinate process anteriorly and posterior portion inserting on Eb4 uncinate process posteriorly, with fibers passing between uncinate processes and inserting on anterior surface of Eb4 just ventral to tip of uncinate process. ② OD3' absent.

OP dorsally on Eb4 posteriorly beginning medially near end of bony surface and extending laterally to just medial to uncinate process; ventrally on Cb5 beginning laterally as broad CT raphe with mid-posterior surface of Ad5 and continuing medially about same extent as muscle occupies on Eb4.

GFM1–3 each begin as fragile sparse muscle fan on anterodistal surfaces of respective Eb and Cb. GFM1 continues dorsoanteromedially a short distance on Eb1. GFM2 continues dorsomedially becoming dorsal and more compact and inserting on lateral surface of tiny, bony diagonal strut anterior to LE2 insertion (TEb2 inserts on medial surface of strut). GFM3 follows path similar to GFM2, ending near OD3'. ② OD3' absent.

Ad4 dorsally begins on Eb4 dorsoposteriorly lateral to LP insertion, extends medially to uncinate

process, with few muscle strands continuous with LP posteroventrally and others joining raphe with LE4 posteromedially; ventrally, muscle attaches on Cb4 dorsally beginning just medial to medial end and extends medially about a quarter length of Cb4. ② Muscle completely separated from LE4 and LP.

Ad5 on Cb4 and dorsoposterodistally and ventrally on Cb5 beginning dorsodistally and extending medially slightly less than distance occupied by Ad4; posterior surface joins broad CT raphe with OP ventrally.

SOD present.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to posteroventrally extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. AC4 present on both sides, but present on only one side and in two pieces in cleared and stained specimen. Neither AC4 nor any indication of a posterior cartilaginous extension of distal end of Cb5 present in ②.

Labroidei

CICHLIDAE

Caquetaia kraussii (Steindachner), USNM 258004, 62.8 mm.

Plate 159

Additional material (lengths not recorded). *Astronotus ocellatus* (Agassiz), USNM 329642; *Cichla ocellaris* (Bloch and Schneider), USNM 226019; *Cichlasoma bimaculatum* (Linnaeus), USNM 181457; *Copadichromis jacksoni* (Iles), USNM 261845; *Crenicichla alta* Eigenmann, USNM 226024; *Cyrtocara moorii* Boulenger, USNM 280311; *Santanoperca leucosticta* (Müller and Troschel), USNM 289647; *Paratilapia polleni*, USNM 344609; *Ptychochromoides katria* Reinthal and Stiassny, USNM 344607; *Ptychochromis oligacanthus* (Bleeker), USNM 344605.

Remarks. Muscles of all the taxa are generally similar. The nature and relationships of LE4, LP, and OP, however, are particularly complex (see discussion in Additional remarks), and variable among the taxa. The description of these three muscles is based almost entirely on *Caquetaia*. Only a few variations pertaining to the other muscles are mentioned in the description.

Description.

LE1 on and lateral to Eb1 uncinate process.

LE2 on Eb2 mid-dorsoposteriorly.

LE3 on Eb3 uncinate process ventral to tip and at OD3–4 attachment to Eb3.

LE4 essentially free, inserting on Eb4 only at point posterolaterally where LE4 joins with LP insertion medially; continuous ventrally with central portion of

OP (separation shown by a raphe), which inserts on Cb5.

LP on Eb4 laterally, insertion fusing with LE4 medially and partly joining raphe with putative lateral part of OP dorsally.

LI1 on Pb2 dorsoanteriorly and Pb3 ventroanteriorly (sandwiched between Pb2 and Pb3).

LI2 dorsolaterally on Pb3 lateral to OD3–4 origin and medial to medial end of Eb3.

TD comprises TPb2, TPb2a, TEb2 and TPb3–Eb4. TPb2 is deeply notched mid-anteriorly and almost completely divided mid-longitudinally; the division is an expansion of the mid-longitudinal raphe frequently present in the acanthomorph TD. The division also completely divides TEb2, but not TPb3–Eb4. TPb2 attaches to Pb2 dorsoanterolateral process (process not visible externally) and to tiny IAC; posteriorly, TPb2 joins CT sheet that covers Pb3 articulating surfaces. TPb2a has mid-anterior raphe and attaches to anterior Pb2 surfaces ventral to TPb2; CT extends posteriorly from raphe and passes between Pb2s and Pb3s; separation of TPb2 from TPb2a is indistinct (but separation may be distinct in other cichlids). TEb2 a pair of muscles, joined medially by CT sheet covering Pb3 articulating facets, and attaching laterally on Eb2 to position anterior to LE2 insertion. TPb2 and TEb2 well separated, not continuous posteriorly with TPb3–Eb4. TPb3–Eb4 attaches on Pb3 posterolaterally slightly ventral to attachment to posteromedial end of Eb4 and continues slightly anteromedially on Pb3. Posteriormost component in some other cichlids attaches only to Pb3 (see also Table 9; and discussion in Additional remarks).

CPb comprises a pair of well-developed sub-epithelial muscles (Anker, 1978:261), each originating posterolaterally on UP4, muscle divides anteriorly with branch attaching to Pb2 laterally and branch passing medially and attaching to Pb3 anteromedially.

OD3–4 origin on Pb3 articulating facet anterolaterally, insertion on medial edge of Eb3 uncinat process and on medial edge of, and enveloping Eb4 uncinat process, joins raphe posteroventrally with a OP medial portion.

OP comprises four parts (apparently not all mentioned or illustrated in the literature; see discussion in Additional remarks): OP1, OP2, OP3, and OP4. The first three parts attach ventrally near the distal end of Cb5 and the fourth part attaches ventrally, broadly on Cb5 dorsally medial to the distal end. OP1 (appears to be the same as Aerts's (1982:233) pars lateralis) is dorsally on Eb4 posteriorly just medial to the membranous dorsal attachment of Ad5; dorso-posteromedially it joins a small raphe with LP ventroposteriorly and is continuous ventromedially with OP2 and ventrolaterally with Ad5. OP2 (the same as Aerts's (1982:233) pars centralis) is continuous with

LE4 ventrally, their junction indicated by a raphe. OP3 is on Eb4 dorsally, extending broadly medially from the uncinat process and joining a raphe with OD3–4 (dorsal attachment appears to be similar to Aerts's (1982:233) pars medialis). OP4 is on most of the posteroventral edge of Eb4 (ventral attachment appears to be similar to that of Aerts's (1982:233) pars medialis).

Ad1 small, on Eb1 anterolaterally and Cb1 anterodistally.

Ad2 and Ad3 well developed, on anterolateral half of respective Eb and anterodistally on respective Cb.

Ad4 (not visible in illustration) dorsally, broadly on Eb4 ventral surface, fusing posteriorly with OP4 dorsoanteriorly, ventrally, narrowly on Cb4 dorsal surface medial to Eb4–Cb4 joint.

Ad5 dorsally, tendinously primarily on posterolateral end of Eb4, secondarily on posterodistal end of Cb4 dorsally; ventrally on posterodistal end of Cb5.

SOD absent, but strap-like branch of SO arises laterally on each side and attaches to Pb3 mid-posteroventrally, giving impression of an interrupted SOD.

RDs adjacent.

Additional remarks. SCL free from Bb3 (SCL absent in *Cichla* and *Crenicichla*). TV4 with continuous ventral portion across Cb5 and split dorsal portion attaching laterally to each Cb5 anteriorly (ventral portion absent in *Cichla*; also reported absent in various African cichlids by Stiassny, 1992:265–267). Pb4 absent, UP4 present. IAC present, small.

Anker (1978) termed our TPb2 as *M. craniopharyngobranchialis* 2 and our TPb2a as *M. transversus pharyngobranchialis* 2. Both muscles appear to be derived from TPb2, and the second, which is not always separate from the first in cichlids, should not carry the main part of the name. TPb2a in acanthomorphs is a specialized part of TPb2 that is restricted to "labroid" (sensus Stiassny and Jensen, 1987), pseudochromid, atherinomorph, and pholidichthyid fishes, and is questionably synapomorphic for these fishes as group.

Anker (1978:256–257) described the musculature of the cichlid *Haplochromis elegans* Trewavas. He termed the posteriormost TD element the *transversus epibranchialis* 4, and described it as attaching to Pb3, Pb4 [actually UP4, Pb4 is absent], and Eb4. Stiassny (1981:96), who examined the dorsal gill-arch musculature in several cichlids (including some genera we also examined), followed Anker in recognizing a TEb4. She appears to have noted no variation in the attachment of this muscle, which she described as originating "from the caudal eminence formed at the junction of Pb3 and UP4." In cichlids there is a tight association of UP4 dorsally with Pb3 at the joint of Pb3 with the medial end of Eb4, and the three elements are bound by CT. The posteriormost TD muscle is attached to this complex dorsally, and as such

is removed from UP4. The posteriormost TD muscle never attaches to the bony portion of UP4, but may attach to Eb4 and Pb3 or only to Pb3 (Table 9).

Remarks. Aerts (1982) studied the development of OP and LE4 in *Haplochromis elegans* Trewavas. He reported that during ontogeny OP forms in three parts (lateral, central, and medial) and that LE4, which is initially separate, combines with the dorsal fibers of the OP medial part. Claeys and Aerts (1984) discussed further the ontogeny of LP, LE4, and OP in *H. elegans* (which they placed in *Astatotilapia*). They found that during ontogeny a few fibers of LP attach dorsolaterally to Eb4, but most become attached to the aponeurotic system of Eb4 dorsolaterally directly opposite the insertion area of the lateral bundle of OP and later join end to end with them to form a compound muscle. Thus, for *H. elegans*, and many or most other cichlids, the "sling" comprises LE4, OP2, and LP, although we find that the contribution of LP to the sling is usually considerably more limited than that of LE4. We further note that OP1 may fuse almost completely with Ad5 (e.g., *Ptychochromis*).

POMACENTRIDAE

Dischistodus fasciatus (Cuvier), USNM 328190, three specimens, 57.1–68.9 mm; USNM 179622, 79.7 mm.

Plate 160

Additional material. ② = *Abudefduf sexfasciatus* (Lacepède), USNM 221863, 68.4 mm; ③ = *Chromis amboinensis* (Bleeker), USNM 338153, not measured.

Plate 161

Remarks. We also recorded limited data on the dorsal gill-arch musculature of several other species (data variably combined or assigned to individual species as warranted): *Acanthochromis polyacanthus* (Bleeker), USNM 275349, 309487; *Amblyglyphidodon aureus* (Cuvier), USNM 338213; *Amphiprion alwardi* Klausewitz, MCZ 4489 (Stiassny and Jensen's (1987) specimen), USNM 275417; *A. melanopus* Bleeker, USNM 338150; *Chromis atrilobata* Gill, USNM 321208, *C. cyanea* (Poey) (USNM 318909), *C. iomelas* Jordan and Seale (USNM 338155; *C. ternatensis* (Bleeker), USNM 338158; *C. viridis* (Cuvier), USNM 338160; *Chrysiptera taupou* (Jordan and Seale), USNM 338076; *Dascyllus reticulatus* (Richardson), USNM 338175; *Lepidozygus tapeinosoma* (Bleeker), USNM 97140, 265252, 275893, 348198; *Mecaenichthys immaculatus* (Ogilby), USNM 215191; *Microspathodon chrysurus* (Cuvier), USNM 194045; *Plectroglyphidodon dickii* (Liénard), USNM 338219; *Pomacentrus vaiuli* Jordan and Se-

ale, USNM 338226; *Stegastes fasciolatus* (Ogilby), USNM 338222.

Description.

LE1 broadly on Eb1 uncinat process ventroanteriorly.

LE2 finely tendinously on bony tip of dorsally expanded posterior edge of Eb2.

LE3 finely tendinously on tip of Eb3 uncinat process medially.

LE4 on dorsal edge of Eb4 lateral to uncinat process, joining raphe with OP dorsal to level of Eb4; LE4 joined ventrolaterally by LP, which does not join OP. ② Lacks raphe with OP. ③ Tendinously on dorsolateral edge of Eb4, does not join raphe ventrally with OP. (See also Discussion following Additional remarks.)

LP finely tendinously on Eb4, joining LE4 posterolaterally. (See also discussion following Additional remarks.)

LI1 by slender tendon mainly on Pb2 dorsoanteriorly just below broad cartilaginous tip of process articulating with IAC, tendon extending secondarily onto CT binding adjacent anteriormost end of Pb3 with Pb2.

LI2 on Pb3 dorsolaterally ventral to medial end of Eb3.

TD comprises TPb2a, TPb2 (see Discussion of TPb2 following Additional remarks), TEb2, and TPb3. TPb2a attached to anterior surfaces of Pb2s; attached mid-posteriorly to CT that passes between Pb3s. TPb2 and TEb2 each comprising a pair of muscles (TPb2 dorsal to TEb2) joined medially by broad area of CT. TPb2 attaching anteriorly to dorsoanterior tip of Pb2. TEb2 of each side attaches to ventrolateral edge of CT connecting TPb2s, muscle extends laterally and attaches on Eb2 dorsally anterior to LE2 insertion, joining medial end of Ad2. TPb3 on dorsoposterolateral end of Pb3 opposite medial end of Eb4. ② TEb2 may just fail to reach medial edge of LE2 or just reaches point anterior to LE2. ③ Similar to *Dischistodus*, but has TPb3-Eb3 instead of TPb3; attachment to Eb3 is to posteromedialmost tip.

Remarks. See discussion in remarks following description of TD in *Parahollardia* (Triacanthodidae) for discussion of similarity of knob-like process attaching Pb3s to ventral surface of skull in that taxon and pomacentrids, and difference from that of labrids, embiotocids, and cichlids.

CPb fibers relative fine, closely bound and obscured by covering CT of pharyngeal area; originating from longitudinal SO fibers passing posteriorly along medial surfaces of Pb2 and Pb3, branching posteriorly and extending along posterior surfaces of Pb3 and UP4 and attaching to posterolateral corner of UP4; another fine strap of muscle attaching to posterior surface of Pb2 and extending laterally around

Pb3 and UP4, and attaching to posterolateral corner of Pb4. ② CPb absent. Absent also in *Lepidozygus tapeinosoma*.

Remarks. This muscle is very difficult to find, and may not be present in most genera. In large specimens of large species, such as *Plectroglyphidodon dickii*, it is relatively easy to find.

OD3–4, OD3' origin on lateral surface of Pb3 dorsal articulating facet (facet partially ventral to TPb2), insertion on medial edges of Eb3 and Eb4 uncinat processes; OD3' questionably identified here as thin layer of fibers originating on Pb3 laterally immediately ventral to OD3–4 origin and inserting dorsally on medial end of Eb3. On only one side of one of four specimens, insertion extended dorsolaterally on Eb3 to point about halfway between medial end of Ad3 and base of uncinat process.

Remarks. We also found OD3' in *Acanthochromis polyacanthus*, *Amphiprion allardi*, and *Lepidozygus tapeinosoma*. It probably occurs in its shortened, specialized state in most or all pomacentrids. The muscle is difficult to find as it is thin, completely overlain by OD3–4, and easily damaged when cutting through OD3–4 to expose the insertions of LI2 and TPb3.

OP dorsally joining raphe with LE4, dorsoanteriorly attached to Eb4 posteriorly beginning medial to uncinat process and extending laterally close to lateral end of Eb4, divided into lateral and medial sections by long slender tendon, which extends from near dorsal end of muscle to dorsodistal end of Cb5; tendon joined laterally by ventromedial end of Ad5. ③ Not continuous dorsally with LE4, comprising broad lateral and slender medial sections, which fuse ventrally and attach to Cb5 dorsoanteriorly, there also joining Ad5.

Ad1–3 each begin on dorsoanterior surface of respective Eb and extend broadly onto anterior surface of joint with respective Cb1, then continue as slender GFM along most of remaining Cb anterior edge.

Ad4 dorsally broadly on ventral surface of Eb4 lateral to uncinat process, ventrally on Cb4 dorsoanteriorly medial to Eb4–Cb4 joint.

Ad5 dorsally broadly on posterolateral surface of Cb4, ventrally broadly on posterolateral surface of Cb5 extending dorsally and joining tendinous extension at ventrolateral end of OP.

SOD absent.

RDs well separated.

Additional remarks. SCL free from Bb3. TV4 in two sections, ventral section relatively thin, continuous across fused Cb5s ventrally; dorsal section thick, interrupted, attaching to lateral surfaces of Cb5 keel. Pb4 absent, UP4 present. Eb4 levator process absent (present, at least, in *Lepidozygus* and *Amphiprion*). See Table 8 for distribution of ACs in pomacentrids.

Discussion. One of Stiassny and Jensen's (1987:

282) main synapomorphies of the Labroidei, is that the dorsal articulating Pb3 facets are completely naked and directly ("bone to bone") contact a ventrally rounded neurocranial apophysis on the base of the skull. They contrasted this condition with that of several families (Gerreidae, etc.) in which the central portion of TPb2 replaced by CT covering Pb3s dorsally. They (1987:276) reported that pomacentrids lack cranio-pharyngobranchialis 2 (= our TPb2; their transversus pharyngobranchialis 2 = our TPb2a), presumably based on the alcohol preserved material they listed (* denotes taxa we also examined): *Abudefduf trocheli* (Gill), *A. saxatilis* (Linnaeus); *Amphiprion allardi**; *Chromis atrilobata**, *C. cyanea**; *Microspathodon chrysurus**; *Neopomacentrus sindensis*; *Pomacentrus otophorus* (= *Stegastes otophorus* (Poey)), *Pomacentrus** *moluccensis* Bleeker; *Stegastes** *acapulcoensis* (Fowler). All the pomacentrids we examined have TPb2 (and TPb2a) similar to that illustrated in Plate 160), with the central portion comprising a broad band of CT covering the Pb3 facets. We thought, perhaps, that Stiassny and Jensen might have considered the reduced pomacentrid TPb2 as part of TEb2, but other than the levator sling, they did not illustrate the pomacentrid muscles, citing illustrations in Stiassny's (1980) Ph.D. dissertation, which is not readily available, and Kauffman and Liem (1982:figs. 2A, 2B). Stiassny kindly sent us a copy of her illustration of the muscles in *Pomacentrus*, and it does not include TPb2, nor do Kaufman and Liem's illustrations.

Among the pomacentrids they examined, Stiassny and Jensen (1987:284 and fig. 8c) reported that LE4 is not continuous with OP in *Chromis* (based on *C. atrilobata* and *C. cyanea*), *Neopomacentrus* (based on *N. sindensis* (Day)) and *Amphiprion* (based on *A. allardi*). LE4 is continuous with OP in our specimen of *C. cyanea*, but not in our specimens of *C. atrilobata* and *C. amboinensis*. Considering the configuration of LE4 and LP in their illustration (the two muscles insert together very narrowly), Stiassny and Jensen appear to have based their description only on *C. atrilobata*.

Stiassny and Jensen (1987:290) reported that LP "never contributes to the muscle sling" in pomacentrids. We examined *Amphiprion melanopus* and *A. allardi* (Stiassny and Jensen's specimen of *A. allardi* was in too poor condition to determine the state of LE4 and OP). In contrast to Stiassny and Jensen, we found that not only LE4, but also LP is broadly continuous with OP in both species of *Amphiprion*, and that LP also contributes to the sling in *Plectroglyphidodon dickii* and *Stegastes fasciolatus*.

Among the four specimens of *Lepidozygus tapeinosoma* we examined, a sling may be absent, LE4 and LP may be continuous with OP, or only one or the other may be continuous with OP, but only a few

muscle strands of LP are involved when LP is continuous with OP.

The pomacentrids have not been analyzed cladistically, and we are unable to hypothesize the plesiomorphic state for the muscle sling, which is important for corroborating inclusion of the Pomacentridae in the Labroidei of Kaufman and Liem (1982) and Stiassny and Jensen (1987). In any event, the pomacentrid sling, when present, differs considerably from the sling in the other labroids in being relatively simple. K.L. Tang is preparing a phylogeny of the pomacentrid genera, which was not available at the time we were preparing our study. We have arbitrarily selected *Dischistodus*, in which the sling consists of LE4 + OP, the most common state, and *Amphiprion melanopus* (not illustrated), in which the sling comprises LE4 (not released from Eb4), LP, and OP, for inclusion in the cladistic analysis. The absence of a sling in *Chromis* and *Lepidozygous*, appears to be specialized in those two genera, because the other, more common character states are either shown by some species of *Chromis*, or other specimens of the monotypic *Lepidozygous*.

EMBIOTOCIDAE

Amphistichus argenteus Agassiz, USNM 132403, 3 specimens, ca. 100+ mm, of which one is cleared and stained, and one damaged.

Plates 162.1, 162.2

Additional material. ② = *Embiotoca lateralis* Agassiz, USNM 340889, 86.8 mm.

Plate 162.1

Additional material. *Cymatogaster aggregata* Gibbons, USNM 340888; *Hysteroecarpus traskii* Gibbons, USNM 61189; *Phanerodon atripes* (Jordan and Gilbert), USNM 337459; *P. furcatus* Girard, USNM 126843 & 337461; *Rhacochilus vacca* (Girard), USNM 340884, *Zalembeius rosaceus* (Jordan and Gilbert), USNM 337463. Most of the information on these taxa is found only on Table 9.

Description.

LE1 broad based, on dorsalmost edge and surface of Eb1 near medial end of element (see Additional remarks for comment about presence of Eb1 uncinate process).

LE2 on mid-dorsoposterior bony edge of Eb2.

LE3 dorsoanteriorly on Eb3 uncinate process, fusing anteroventrally with OD3–4.

LE4 complex, massive, essentially free from Eb4, fused posterolaterally with LP dorsal to Eb4, joining raphe with presumable middle section of OP.

LP laterally on Eb4 posterolaterally, fused with LE4 ventroanteriorly, joining raphe ventrally with presumable middle section of OP. ② LP more distinct,

on levator process dorsally, continuous posteroventrally by only a few muscle strands with OP.

Remarks. There is a strong, bony process that bears the cartilage tip of the levator process in ②. The same process is present in *Amphistichus*, which lacks the cartilage (hence, uncinate process absent).

LI1 on dorsomedial surface of Pb2 and dorsoanterior surface of Pb3. ② On Pb2 dorsally.

LI2 inserts by long tendon on Pb3 dorsoposterolaterally ventroanterior to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 a pair of muscles joined medially by CT to ventrolateral surface of CT pad covering otherwise naked dorsal Pb3 articulating facets, extending laterally on dorsal surface of Eb2 anterior to LE2 insertion, joining raphe with medial end of Ad2. TPb3-Eb4 on Pb3 dorsoposterolaterally, a little medial to LI2 insertion, continuing posteriorly and attaching to medialmost edge of Eb4, thence continuing along posteromedial surface of Eb4 and joining raphe with dorsomedial edge of a branch of OP (possibly the same as either OP3 or OP4 of cichlids). TPb3-Eb4 posteromedially, continuous mid-posteriorly with SOD. ② TEb2 does not join raphe with Ad2.

CPb absent, but, unusually, SO, which is covered ventrally by pharyngeal roof CT, spreads anterolaterally (Plate 162.2) and lines the ventral surfaces of the epibranchials (see M. Pb3-UP4).

Remarks. Muscle questionably distinct from loose mix of SO + CT fibers that spreads over pharyngeal roof, and is possibly homologous with one or all of the muscles identified as CPb in other putative labroids and pholidichthyids, callionymoids, centrogeniids, lethrinids, pseudochromids, nemipterids, and sparids. Muscle fibers do not attach to the (reduced) Pb2s or pass around them anteriorly, as they do in the other taxa.

M. Pb3-UP4 ventral to RD, on Pb3 ventroposteriorly and UP4 ventroanteriorly (also present in ② and *Cymatogaster*, but not other genera examined).

OD3–4 originating on lateral surface of Pb3 dorsal articulating facet, inserting massively on dorsomedialmost surface of Eb3 and anterior surface of uncinate process (there joining LE3 insertion anteriorly) and medial edge of bony Eb4 uncinate process.

OP complex, presumably comprising two or three sections (only two indicated here): posterior section joining raphes dorsally with LE4 and LP, ventrally on Cb5 distally, joining tendinous raphe laterally with Ad5; anterior section broad, on Eb4 posteriorly, fusing posteriorly with anterior section ventral to Eb4.

Ad1–3, each broad, on anterolateral surfaces, covering joint, of respective Eb and Cb.

Ad4 thin muscle sheet dorsally on ventrolateral edge of Eb4 and ventrally narrowly on Cb4 dorso-

laterally, obscured from view by OP portion attaching broadly to Eb4 posteriorly.

Ad5 dorsally on tiny AC4 (not visible in illustration), narrowly on Cb4 distally, and broadly on Eb4 posterodistally; ventrally on Cb5 distal end, joining tendinous raphe with OP posterior section. ② Slight, conformational separation of Ad5 from OP along raphe.

SOD present. ② Absent. See also Additional remarks.

RDs slightly separate.

Additional remarks. SCL attached mid-dorsally by long tendon to posteroventral end of Bb3. TV4 complex, but dorsally attached to Cb5, ventrally continuous but interrupted by raphes, possibly comprising separate dorsal and ventral sets of muscles. Pb4 absent, UP4 present. Pb1 cartilaginous. Pb2 edentate.

The uncinate process of Eb1 appears to have moved medially and essentially become confluent with the medial end of the anterior arm of Eb1 in all embiotocids, hence, a synapomorphy for the family. Evidence for this assumption is that Pb1 articulates with the rounded ventral portion of the cartilaginous medial end of Eb1 and a ligament connects the dorsal, blade-like cartilaginous medial edge of Eb1 to Pb2.

Tiny ACs present as follows (Table 8): *Amphistichus argenteus*, AC4 present on one side of each of two specimens (of which one cleared and stained; third specimen damaged), Ad5 attached to it in one specimen; *Phanerodon atripes*, AC4, Ad5 not attached to it; *P. furcatus*, AC1 and AC2 present or absent; *Zalembeius rosaceus*, AC4, Ad5 attached to it.

SOD in *Amphistichus* is distinct and readily recognizable. In both species of *Phanerodon*, however, SOD arises from SO dorsolaterally as a short, fine strip of muscle that fuses with the ventrolateral surface of TEb4, and is easily overlooked. Stiassny and Jensen (1987), who examined *Phanerodon*, but not *Amphistichus*, reported that all labroids, in which they included embiotocids, lack SOD. Presence of SOD is generally plesiomorphic for percomorphs and possibly indicative that *Amphistichus* is one of the most plesiomorphic genera in the family. The state of SOD in *Phanerodon* appears to be more specialized.

Liem (1986) illustrated and described the gill-arch musculature of *Embiotoca lateralis*. Our observations are in general agreement with his; however, Liem described LI1 as inserting only on Pb2, and LP as completely separate from LE4. We examined Liem's material (MCZ 58890) and find that LI1 and LP accord with the description of our specimen.

Labroidea

In order to facilitate discussion of the unquestionably monophyletic group comprising the Labridae,

Table 10.—Distribution of certain characters in genera of labroid fishes. Dash (–) = absent; P = present; C = continuous; D = divided; F = fused; S = separate.

Genera	LE3'	TEb1	TEb2	TPb3-Eb4	RD
Labridae					
<i>Achoerodus</i>	-	-	-	C	F
<i>Bodianus</i>	-	P	PA	C	F
<i>Cheilinus</i>	-	P	PA	C	F
<i>Cheilio</i>	-	-	A	C	F
<i>Choerodon</i>	P	-	A	C	F
<i>Clepticus</i>	-	P	P	C	F
<i>Coris</i>	P	-	P	C	S
<i>Decodon</i>	-	P	A	C	F
<i>Halichoeres</i>	-	-	PA	C	S
<i>Hologymnosus</i>	-	-	P	C	S
<i>Labroides</i>	P	-	P	C	S
<i>Notolabrus</i>	-	-	P	C	S
<i>Polylepion</i>	P	P	P	C	S
<i>Pseudodax</i>	-	?	?	C	F
<i>Pseudolabrus</i>	-	-	P	C	S
<i>Semicossyphus</i>	-	P	A	C	S
<i>Suezichthys</i>	-	-	A	C	S
<i>Symphodus</i>	-	P	A	C	F
<i>Tautoga</i>	-	P	A	C	F
<i>Tautoglabrus</i>	-	P	P	C	F
<i>Xiphocheilus</i>	-	P	A	C	F
Odacidae					
<i>Odax pullus</i>	-	P	P	C	F
Scaridae					
<i>Leptoscarus</i>	-	P	A	D	F
<i>Nicholsina</i>	-	P	A	D	F
<i>Sparisoma</i>	-	P	A	D	F

Odacidae, and Scaridae, and distinguish them from other families (Embiotocidae, Pomacentridae, Cichlidae) included in the putatively monophyletic suborder Labroidei, we use the superfamily name Labroidea. The Labridae are generally considered the least specialized of the three families and, for the most part, we restrict our description and discussion to them.

Additional material. We examined the gill-arch muscles of several taxa of Labroidea other than the labrids described in the detailed accounts (data on these taxa are included in Tables 8–10): LABRIDAE: *Bodianus mesothorax* (Bloch & Schneider), USNM 217854; *Bodianus rufus* (Linnaeus), USNM 320990; *Cheilinus trilobatus* Lacepède, USNM 224020 (**Plate 167B**); *Cheilio inermis* (Forsskål), USNM 114811, 332257; *Choerodon graphicus* (De Vis), USNM 218548 (**Plate 167A**); *Choerodon cyanodus* (Richardson), USNM 328226; *Clepticus parrae* (Bloch & Schneider), USNM 318548 (**Plate 167C**); *Decodon puellaris* (Poey), USNM 185260; *Halichoeres margaritaceus* (Valenciennes), USNM 334551; *Halichoeres hortulanus* (Lacepède), USNM 336931; *Hologymnosus doliatus* (Lacepède), USNM 218484; *Notolabrus celidotus* (Bloch & Schneider), USNM

339231; *Polylepion cruentum* Gomon, USNM 215466; *Pseudolabrus miles*, USNM 339193; *Pseudodax moluccanus* (Valenciennes), USNM 295262; *Semicossyphus pulcher* (Ayres), USNM 338987; *Suezichthys aylingi* Russell, USNM 339187; *Symphodus roissali* (Risso), USNM 198879; *Tautoga onitis* (Linnaeus), USNM 118352, 163713; *Tautogolabrus adspersus* (Walbaum), USNM 118349; *Xiphocheilus typus* Bleeker, USNM 260876; ODACIDAE: *Odax pullus* (Forster), USNM 339188; SCARIDAE: *Sparisoma aurofrenatum* (Valenciennes), USNM 319033; *Leptocarus vaigiensis* (Quoy & Gaimard), USNM 330153; *Nicholsina denticulata* (Evermann & Radcliffe), USNM 202270.

Common and other characters. Many aspects of the musculature of the taxa are similar (e.g., all have LE1–3, LI1, LI2, TPb3–Eb4, Ad1–3; all but *Bodianus* have CPb). They differ mainly in the composition of the anterior TD muscles (Tables 9 and 10), whether the RDs are fused ventrally (underlain by a strap of CT) at least to a point just posterior to their insertion on Pb3s, or are separate, whether TPb3 is continuous from one side of the gill arches to other (or whether it is interrupted at the mid-line), and whether a sling (Stiassny and Jensen, 1987:283–284, fig. 8) is present (absent only in *Labroides*).

An interrupted TPb3–Eb4 is a scarid synapomorphy (hence, the problematic *Pseudodax* does not belong in the scarid clade and possibly merits a family-group name equivalent to Labridae, Odacidae, and Scaridae).

One character, *LE1 insertion includes area medial to the Eb1 uncinat process (usually entirely medial), is a synapomorphy of the Labroidea* among all acanthomorphs (we exclude the peculiar state in *Cololabis* (Scomberesocidae, Plate 100) in which LE1 extends medially along a tendon from the tip of the uncinat process, but is restricted, nevertheless, to an area well medial to the medial end of Eb1). Only in the highly specialized labrid, *Labroides*, is the insertion on and lateral to the uncinat process, a condition we consider specialized within the Labroidea. A problem concerning this character is provided by taxa lacking an Eb1 uncinat process. In most, if not all, of the problematic taxa, except possibly the labroid family Embiotocidae, the insertion is well removed laterally from the medial end of Eb1 and probably indicates that the muscle insertion has not moved medially. The insertion in the embiotocids, which lack an uncinat process, is close to the medial end of Eb1, and is possibly indicative of a close relationship between Labroidea and Embiotocidae.

Choerodon (Plate 167A) is unique in that LE1 comprises two separate muscles (LE1, LE1'), one which inserts entirely medial to the uncinat process, and the other, which inserts just ventrolateral to the tip of the uncinat process. Such a condition could

develop from the typical labroidean condition by loss of the central portion of the typical LE1. Loss of the medial portion would result in a condition similar to that of *Labroides*.

LE2'. We consider the distinction between LE2' and LE2 to be problematic. LE2' only occurs in the presence of LE2, and is possibly an artefact of dissection. Eb1 and Eb2 are closely juxtaposed in labrids. In most labrids, a tendon extends along LE2 from about mid-length to insertion on a bony process on the posterior margin of Eb2. At this point the tendon continues as a ligament attaching to a process on the anteroventromedial margin of Eb3. In many labrids, it appears that the LE2 comprises two separate elements, one (LE2) inserting musculously and the other tendinously on Eb2. In attempting to decide whether one or two muscles are involved, it is necessary to force apart Eb2 and Eb3. In doing this, the questionable muscle sometimes remains entirely on Eb2, sometimes it appears to divide, but remain on Eb2, sometimes it appears to completely separate and be associated only with Eb3. In *Tautoga* and *Pseudodax*, LE2 is clearly restricted to Eb2, with no indication of possible division. In *Choerodon*, *Halichoeres*, and *Notolabrus*, LE2' appears to be present. In the other genera, the situation is questionable.

Transversus dorsalis. The names we apply to the anterior TD muscles should be considered highly tentative. As much as possible, we identify these muscles with those commonly found among acanthomorphs.

One example of how a pair of muscles can vary is exemplified by *Coris*, *Choerodon*, and *Xiphocheilus*. The lateral attachments of TPb2 and TPb2a in *Coris* (Plate 166) are to the anterolateral tip of Pb2, the most common attachments of these two muscles in labrids. In *Choerodon* (Plate 167A), TPb2 appears to have shifted its attachment to the tip of the Eb3 uncinat process, and the anterior portion of TPb2a appears to have an anterior branch that also attaches to the process. In *Xiphocheilus* (not illustrated), it appears that the condition in *Choerodon* has been carried one step further, and the TPb2a portion has been lost. We have arbitrarily indicated the muscles in *Choerodon* and *Xiphocheilus* as TPb2 and TPb2a in Table 9 and on Plate 167A. A study of the dorsal gill-arch musculature of labroideans will probably uncover informative characters for intra- and inter-familial relationships.

Transversus epibranchialis 1. Unaware, perhaps, that some labrids lacked TEb1, Stiassny (1980:248–249) proposed that the presence of TEb1 is a synapomorphy of the Labridae. A cladistic analysis of the Labridae will be required in order to determine whether the absence of TEb1 in Labridae is a secondary loss. Pending such an analysis, we treat the lack of TEb1 in labrids as the plesiomorphic state.

Pharyngobranchial 1. Our identification of Pb1 in labrids, the only labroideans that have an element that might be interpreted as Pb1, is problematic. All labrids we examined, except *Labroides*, have such an element, which is always cartilaginous. Pb1 is unambiguously absent in *Labroides*, which is clearly a specialized state for an acanthomorph. In the other labrids, there is a range of variation in morphology of the cartilage at the anteromedial end of Eb1: an unremarkable cartilaginous end joining a separate, curved or straight rod-like cartilage (e.g., *Achoerodus*, Plate 163.1A; *Polylepion*, Plate 165A), which might be interpreted as Pb1; a greatly expanded, medially flattened cartilage cap giving rise anteriorly to a continuous, posteriorly directed, curved cartilage rod (e.g., *Coris*, *Halichoeres*), which might be interpreted either as Pb1 fused to the end of Eb1 or as a *de novo* shape of the anteromedial end of Eb1; a greatly reduced autogenous filament of cartilage, which may be present on one side and absent on the other, and which might also be interpreted as Pb1.

In the two specimens of *Coris* (USNM 337450), the cartilaginous medial end of Eb1 is basally cuboid and medially plate-like with the anterior margin forming a worm-like, dorsally extending process. Evidence that the process originates as part of the plate-like portion is indicated by the conditions in USNM 92292. On the left side of this specimen the plate-like portion is almost completely demarcated from the remainder of the cartilaginous end of Eb1 by a line of unstained tissue, as precedes the budding off of cartilaginous ACs. On the right side, there are two isolated non-staining areas in the same relative position as the unstained line on the left side. The unstained areas appear to mark the budding off of the putative Pb1. The situation in labrids is unusual, however, in that developmentally, Pb1 appears to form separately from the medial end of Eb1 in the earliest ontogenetic stages of perciforms (e.g., Pott-hoff et al., 1987, pomacentrid), if not all acanthomorphs.

Like the presence or absence of TEb1, the state of the medial end of Eb1 may offer clues to the intra-familial relationships of the labrids.

Sling. The composition of the sling is also complex, involving LP, LE4, OP, and Ad5 in apparently different ways. Some of the variation in the sling can be gleaned from the illustrations.

LABRIDAE

Remarks. Yamaoka (1978) describes seven origin types for LP, which he associates with feeding types. We did not investigate LP origins.

Achoerodus viridis (Steindachner), AMS I.7019-006, 88.9 mm; USNM 218488, 56.8 mm.

Plates 163.1, 163.2

Description.

LE1 on Eb1 medially beginning laterally ventral to tip of uncinat process and extending to dorso-medial end of Eb1.

LE2 on dorsoposterior edge of Eb2 at mid-length.

LE3 tendinously and muscously on all bony Eb3 and cartilage-tipped Eb4 uncinat processes; muscle twists on itself as it descends from origin.

Remarks. A cartilage tipped Eb3 uncinat process is absent in all labrids. The tip of the Eb4 uncinat process (usually not visible as it is often obscured by LE3 insertion) may be cartilaginous or all bony varying with the taxon and possibly with growth (beginning as cartilage and becoming bony).

LE4 complex, essentially free from Eb4 (except for "point" attachment to Eb4, where LE4 and LP fuse), fused with LP along broad, ventrally extending tendon that attaches to dorsoposterior edge of distal end of Cb5, presumably incorporating middle section of OP ventral to level of Eb4.

LP complex, massive, on dorsal and ventral surfaces of Eb4 (bone appears tilted up so that surfaces could be interpreted as anterior and posterior), extends ventrally fusing with presumed lateral portion of OP.

LI1 on Pb3 articulating surface ventroanterolaterally.

LI2 on Pb3 posterolaterally, ventral to Eb3 medially.

TD comprises TPb2-Pb2a and TPb3-Eb4. TPb2-Pb2a originates posteriorly from anteriorly extending fibers from transverse SO muscle layer passing between naked dorsal Pb3 articulating facets and spreading anteriorly and attaching on dorsoanterior surfaces of Pb2s. TPb3-Eb4 attaches to posterolateral-most surface of Pb3 and ventroposterolmedialmost edge of Eb4.

Remarks. Homology of anterior TD muscles of labrids, odacids, and scarids with those of other acanthomorphs is problematic.

CPb extends from posterolateral corner of Pb3 anteriorly around Pb2 and Pb3 ventral to TPb2-Pb2a to posterolateral corner of opposite Pb3.

OD3-4 origin on lateral surface of dorsal Pb3 articulating facet, insertion on medial edge of bony Eb3 uncinat process and mid-anterior edge of Eb3 ventral to process, and on medial edge of cartilage-tipped Eb4 uncinat process.

OP complex, possibly consisting of three sections; questionable middle section participating in sling as muscle ventral to raphe joining LE4 and LP; lateral section fusing with LP ventrally and Ad5 posteriorly; medial section in two parts: dorsal part on posterior surface of Eb4 ventral to OD3-4, becoming tendinous ventrally and joining broad tendon extending from OP middle section shortly ventral to broad tendon's giving rise to long posteriorly extending liga-

ment; ventral part musculously on posterodistal surface of Cb5, fused with ventral end of lateral OP section and/or posterior surface of Ad5.

Remarks. The OP sections of labrids are possibly homologous with the three OP sections identified in embiotocids and three of the four sections identified in cichlids, but await confirmation from cladistic and embryological studies.

Ad1 spans anterior surface of Eb1-Cb1 joint.

Remarks. Slender GFM1 extends ventrolaterally across Ad1 surface from dorsomedial origin of Ad1; others may have been present on arches 2 and 3, but were not noted during dissection. GFMs were not specifically checked for during dissection of labrids.

Ad2 with two portions joined to raphe; dorsal portion extends from dorsal surface of Eb2 just anterior to LE2 insertion and attaches to posterior surface of Eb1 ventral to uncinat process; ventral portion spreads ventroanteriorly from raphe and attaches to Cb2 anterior surface just ventral to Eb2-Cb2 joint.

Ad3 dorsally on almost entire anterior edge of Eb3 ventroanterior to uncinat process, tendinously attached (not illustrated) to Eb2 at and continuous with LE2 insertion, extending ventrolaterally across anterodistal surface of Cb3 and attaching just ventral to cartilaginous distal end.

Ad4 on Eb4 ventrolaterally and on Cb4 dorsally anterior to Eb4-Cb4 joint.

Ad5 most recognizable dorsolaterally, attaching dorsally broadly, tendinously to Eb4 and Cb4 posterodistally, and ventrally to Cb5 dorsodistally, medial surface fused with OP complex.

SOD absent.

RDs fused, dividing just before attaching to Pb3s.

Additional remarks. SCL attached mid-dorsally by CT to posterior surface of posteroventrally extending cartilaginous tip of Bb3. TV4 mostly split, attached to Cb5s laterally except for thin, continuous muscle strap passing across Cb5s ventrally. Pb4 and UP4 absent. Pb1 cartilaginous. Eb4 levator process absent. See Table 8 for distribution of ACs in labrids.

Symphodus roissali (Risso), USNM 198879, 2 specimens, 50.0–55.8 mm.

Plates 164.1, 164.2

Description (see also remarks following various muscle descriptions under *Achoerodus*).

LE1 broadly on Eb1 beginning at base of uncinat process and extending medially to medialmost bony edge.

LE2 narrowly, tendinously on mid-dorsoposterior edge of Eb2.

LE3 tendinously on tip of Eb4 [sic] uncinat process (Eb3 and Eb4 tightly joined, but muscle has shifted its usual insertion from Eb3 to Eb4).

Remarks. Eb4 uncinat process with minute cartilage tip at bottom of minute, shallow bony depression, as if bone was about to grow over tip.

LE4 essentially free from Eb4, joins LP dorsal to level of Eb4, ventrally continuous with presumed middle section of OP (raphe not illustrated).

LP massive, on Eb4 dorsolaterally, posteroventrally joining raphe (not illustrated) with presumed lateral section of OP, which continues ventrally as broad tendon that attaches to Ad5 and inserts on Cb5.

L11 on anterolateral surface of Pb3 just posterior to dorsoanterior tip of Pb2.

L12 tendinously on posterolateral surface of Pb3.

TD comprises TEB1, TPb2-Pb2a-Pb3, and TPb3-Eb4. TEB1 on mid-anterior edge of Eb1s with fine crossing muscle filaments mid-posteriorly attaching to cartilaginous Pb1s and medial edge of Eb1s. TPb2-Pb2a-Pb3 originating posteriorly as longitudinal fibers extending anteriorly from transverse SO layer, passing between Pb3s, dividing and passing over and attaching to Pb2s and around each Pb3 and attaching to it; dorsal divisions continuous ventrally with uninterrupted portion, which attaches to Pb2s laterally. TPb3-Eb4 attaches to posterior surface of Pb3 dorsal articulating facets and to Eb4s posteromedially.

CPb semicircular band passing anteriorly around, but mostly separated by epithelial tissue from, Pb2 and Pb3 ventral to uninterrupted portion of TPb2-Pb2a-Pb3, attaching to posterolateral corner of Pb3, and continuing posteromedially and meshing complexly with SO.

M. Pb2-Eb2 on Pb2 ventrolateral edge, passing between TPb2-Pb2a-Pb3 and CPb and attaching to small bony process on mid-anterior edge of Eb2.

Remarks. This muscle is possibly a separate extension of CPb. In many other species of labrids, CPb has a fine tendinous attachment to Eb2 ventromedially and Pb2 ventrolaterally as it extends posteriorly, or muscle fibers are continuous with CPb.

OD3 absent.

OD4 on lateral surface of Pb3 articulating facet and Eb4 uncinat process (see remarks following LE3).

OP presumably in three sections: lateral section joining raphe dorsally with LP and continuing ventrally as broad tendon, which joins Cb5 dorsoposteriorly, and is joined by Ad5 anteriorly; tendon continues dorsally, joining OP middle section; medial section on Eb4 posteriorly and Cb5 dorsally medial to broad tendon, medially continuous with SO.

Ad1 broadly on Eb1 and cartilaginous Pb1 dorsally and Cb1 anteriorly well ventral to distal end.

Ad2 on Eb2 dorsomedially and Cb2 anteriorly well ventral to distal end.

Ad3 on Eb3 dorsomedially ventral to OD4 and Cb3 anteriorly well ventral to distal end.

Ad4 dorsally on ventrolateral surface of Eb4, ventrally on Cb4 dorsolaterally medial to Eb4-Cb4 joint.

Ad5 ventrally on dorsoanterodistal surface of Cb5, dorsally broadly on posterodistal ends of Eb4 and Cb4, medially joining tendon from OP middle section.

SOD absent.

RDs fused, separating just before attaching to Pb3s.

Additional remarks. SCL present (cartilaginous posterior end of Bb3 recurved ventrally). TV4 completely divided medially, attaching to Cb5 anterolaterally on each side. Pb4 and UP4 absent. Pb1 cartilaginous. Eb4 levator process absent. See Table 8 for distribution of ACs in labrids.

Polylepion cruentum Gomon, USNM 215466, 82.7 mm.

Plate 165

Additional material. ② = *Coris julis* (Linnaeus), USNM 337450, 2 specimens: 135–164 mm; USNM 92292, 105 mm.

Plate 166

Description.

LE1 on dorsomedialmost edge of Eb1 medial to cartilage-tipped uncinat process. ② Broadly on Eb1 beginning near dorsoposteromedialmost bony surface and extending to base of uncinat process.

LE2 on bony process formed by mid-dorsoposteriore edge of Eb2, joining LE2' insertion. LE2' (See discussion of LE2' in Labroidea section) tendinously on bony process at mid-dorsoposterior edge of Eb2 together with LE2, ligament continues posteriorly from insertion and attaches to bony process on ventroanteromedialmost edge of Eb3. ② On bony process at ventroanteromedialmost edge of Eb3, ligament attaches process to Eb2 process supporting LE2.

LE3 tendinously on tip of all bony Eb3 uncinat process. ② On tips of tightly joined bony Eb3 and cartilage-tipped Eb4 uncinat processes.

LE4 massive, essentially free from Eb4, fusing with LP dorsal to level of Eb4 and presumable middle portion of OP, which continues ventromedially as long tendon and attaches to Cb5, and fuses laterally with Ad5.

LP massive, partly on dorsoanterior surface of Eb4, but mainly on posterolateral surface, where it is joined by LE4; joins raphe ventrally with presumable lateral section of OP.

LI1 on Pb3 dorsoanterolaterally, anteroventral to dorsal articulating facet.

LI2 on Pb3 dorsolaterally anterior to joint with Eb3 medial end.

TD complex, comprising TEb1, TEb2, TPb2, TPb2a, and TPb3-Eb4. TEb1 on dorsoanteromedial

surfaces of Eb1s, anterolaterally joining raphe with Ad1, joined posteriorly by complex muscle strands to CPb; some strands continue posteriorly as bilateral pair of longitudinal SO bands that pass posteriorly between Pb3s and give rise dorsally to two bilateral pairs of small, slender muscles: each member of anterior pair, TPb2, attaches to anterior tip of Pb2 together with TPb2a; each member of posterior pair, TEb2, attaches to Eb2 dorsal surface near medial attachment of Ad2. TPb2a attaches broadly to medial edge of slender anterior Pb2 process. TPb3-Eb4 attaches to posterior surface of Pb3 articulating facets and to posteromedial surface of Eb4. ② TEb1 and associated longitudinal strands of SO absent. TEb2 joins raphe laterally with Ad2.

CPb with broad anterolateral extension attaching to anterior edge of Eb2 ventral to Ad2; muscle otherwise semicircular, with median anterior raphe, passing posterolaterally around Pb2 and Pb3 on each side, thinning and attaching to posterolateral corner of Pb3, thence spreading posteriorly and continuing as SO. ② No median raphe; does not continue posteriorly beyond attachment to Pb3.

OD3–4 origin on anterolateral edge of Pb3 dorsal articulating facet, continuing posteriorly on Pb3 ventral to facet, insertion on medial edges of bony Eb3 and Eb4 uncinat processes. ② Eb4 uncinat process with cartilage tip.

OP presumably comprising three sections; lateral section dorsally joining raphe with LP ventrally and medially joining long tendon that joins middle OP section dorsally, ventrally fusing indistinguishably with Ad5 posteriorly; medial section on distal end of Cb4, becoming tendinous dorsally on one side (remaining muscular on other) and attaching to Eb4 posteriorly. ② Medial OP section absent.

Ad1 broadly on Eb1 dorsoanteriorly beginning at raphe with TEb1 (which is absent in ②), extending ventrolaterally medial to Eb1-Cb1 joint, and attaching to Cb1 anteriorly ventral to joint.

Ad2 broadly on most of bony length of Eb2, extending ventrolaterally just medial to Eb2-Cb2 joint and attaching to Cb2 anteriorly just ventral to joint.

Ad3 broadly on most of bony length of Eb3, extending ventrolaterally just medial to Eb3-Cb3 joint and attaching to Cb3 anteriorly just ventral to joint.

Ad4 broadly on Eb4 ventrolateral edge and Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 ventrally on Cb5 dorsolaterally, dorsally broadly on Eb4 and Cb4 laterally, fused laterally with OP.

SOD absent.

RDs fused ventrally just posterior to attaching to Pb3s. ② RDs separate well posterior to Pb3s.

Additional remarks. SCL attached mid-dorsally to ventrally extending cartilaginous posterior end of Bb3. TV4 completely divided, attaching to Cb5 an-

terolaterally. Pb4 and UP4 absent. Eb4 levator process absent. ② SCL present; cartilaginous posterior end of Bb3 extends ventrally; thin band of TV4 continuous across Cb5 ventral to anterolateral attached portions. See Table 8 for distribution of ACs in labrids.

Labroides dimidiatus (Valenciennes), ① = USNM 309376, 70.7 mm; ② = USNM 205283, ca. 65 mm SL; ③ = USNM 363249, 80.3 mm SL; ④ = USNM 369939, 69.5 mm.

Plate 168

Description (unless noted otherwise, description applies to all four specimens).

LE1 originates tendinously, inserts on bony dorsoanterior surface of Eb1 uncinat process.

LE2 on tip of expanded mid-posterior edge of Eb2, probably joining LE2' ventrally (see remarks following LE2').

LE2' (See discussion of LE2' in Labroidea section) tendinously on bony process ventral to medial end of Eb3 and questionably on mid-posterior edge of Eb2 at or with LE2 insertion.

Remarks. Eb2 is tightly joined to Eb3 posterior to LE2 insertion, and it is difficult to decide whether LE2' actually joins LE2. Eb2 and Eb3 are artificially separated in Plate 168A.

LE3 tendinously on tip of all bony Eb3 uncinat process.

LE4 ribbon-like, on Eb4 dorsolaterally, varying as follows: ① inserting muscously at and anterior to LP on one side and at and posterior to LP on the other; ② fusing with LP (forming a Y) and inserting muscously together (both sides); ③ inserting tendinously at and posterior to LP (both sides); ④ extending tendinously across and joining ventromedial surface of LP and inserting on bony distal end of Eb4 dorsally together with ventroposteromedial surface of LP.

LP ribbon-like, on Eb4 dorsolaterally, variable (see LE4), insertion continuous posteroventrally with CT to which PP (not illustrated) also joins. ④ Muscle fibers are continuous ventromedially with OP on left side but not on right side.

LI1 slender, on Pb3 dorsoanteriorly near articulation with Pb2 dorsal process.

LI2 on Pb3 dorsolaterally ventral to dorsal articulating facet.

TD comprises TPb2-Pb2a, TPb3, TEb2, and TPb3-Eb4. Anterior three muscles originate posteriorly from transverse SO fibers that pass anteriorly between Pb3s and divide on exiting from between Pb3s. TPb2-Pb2a fuses ventrally with uninterrupted transverse muscle portion (dorsal to CPb) and attaches to Pb2s anterolaterally. TEb2 extends laterally posterior

to ascending process of Pb2 and attaches on Eb2 dorsoanteriorly, meeting anteromedial margin of Ad2. TPb3 attaches to Pb3s anterolaterally dorsal to TPb2-Pb2a and along medial edge of Eb2. TPb3-Eb4 attaches medially to posterior surfaces of Pb3 articulating facets and to posteromedial half of Eb4.

CPb, beginning posteriorly, attaches on posterolateral corner of Pb3, extends anterolateral to Pb3 attaching minutely to Eb2s ventroanteriorly, and continues anteromedially ventral to TPb2-Pb2a to opposite side.

Remarks. It was unclear if the Pb2a portion of TPb2-Pb2a was present in ②.

OD3 origin on lateral surface of Pb3 articulating facet, insertion on anterior surface of all bony Eb3 uncinat process.

OD4 origin on lateral surface of Pb3 articulating facet posterior to OD3, insertion beginning on dorsal surface of cartilage-tipped Eb4 uncinat process and extending laterally.

OP on Eb4 ventrolaterally and Cb5 dorsomedial to Ad5.

Ad1-3 similar, muscle on most of dorsoanterior surface of respective Eb, extending anteriorly over Eb-Cb joint and attaching along anterior surface of Cb.

Ad4 (occluded in posterior view) on ventrolateral edge of Eb4 and dorsolateral edge of Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally on cartilaginous distal end of Cb4 continuing as CT with which LP and PP are also continuous; ventrally on Cb5 dorsolaterally.

SOD absent.

RDs well separated.

Additional remarks. SCL present. Except for thin, ventral, continuous section of fibers, TV4 attached to Cb5 anterolaterally. Pb1, Pb4, and UP4 absent. See Table 8 for distribution of ACs in labrids.

Labroides. *Labroides* is the most distinctive of the labroidean genera we examined. It alone lacks a sling and has the LE1 insertion on and lateral to the Eb1 uncinat process. It also lacks TEb1 and has separate RDs. Although, all these characters are plesiomorphic for acanthomorphs, we believe all, except possibly the absence of TEb1, will prove to be apomorphic at various levels within the Labroidea. The continuous portion of LP with OP on one side of one of four specimens, is probably anomalous and, if our interpretation is correct, not homologous with the LE4-OP sling of other labrids.

Pholidichthyoidei

The interrelationships of the Pholidichthyidae remain unresolved. The family shares specializations with a diverse group of fishes. In recent times, it has been questionably or provisionally associated with

the blennioids (Springer and Frehofer, 1976:40), the labroids (Stiassny and Jensen, 1987), and the trachinoids (Nelson, 1994:397).

PHOLIDICHTHYIDAE

Pholidichthys leucotaenia Bleeker, CAS 32408, one very large (illustrated) and one 230 mm SL; USNM 289924 and uncataloged, two juveniles.

Plate 169

Additional material. ② = *Pholidichthys anguis* Springer and Larson, USNM 337860 and NTM S13529-001, both juveniles.

Description.

LE1 inserts by slender tendon on Eb1 anterior to base of uncinat process; ligament (not shown) joins posterior edge of Eb1 to anterior edge of Eb2.

LE2 inserts on tip of bony Eb2 process posterolateral to uncinat process; ligament (not shown) joins process to anterior edge of Eb3. ② Process absent.

Remarks. A low, cartilage-tipped Eb2 uncinat process occurs in some specimens of *P. leucotaenia*, but not others. In some specimens the cartilaginous medialmost end of Eb2 is more anteriorly directed and overrides the dorsal surface of Pb2 (see Springer and Frehofer, 1976:fig. 7, left side of fish), but when articulating with Pb3 is attached to bony surface. Among ctenosquamates, a cartilage-tipped uncinat process on Eb2 occurs elsewhere only in *Hemiramphus*, (Hemiramphidae), in which it does not articulate with another skeletal element.

LE3 inserts on Eb3 uncinat process.

Remarks. Eb3 uncinat process is closely bound by CT to anterior edge of Eb4, which lacks an uncinat process. Because of the tight joint, it is possible to interpret LE3 as inserting on both Eb3 and Eb4, although the attachment seems to favor Eb3. Except for the Lampridae and Veliferidae, LE4 never inserts on the Eb4 uncinat process in acanthomorphs.

LE4 absent.

Remarks. *Pholidichthys*, the gasterosteid *Spinachia*, and the echeneids are apparently the only acanthomorphs that lack LE4.

LP broadly on most of lateral half of dorsoposterior surface of Eb4, insertion posteriorly paralleling and closely approximating OP attachment on Eb4; muscle extends posteromedially towards its origin on the basioccipital, which is well removed from the other levators, which originate together on the pro-otic.

LI1 narrowly on anterolateral edge of Pb3 just posterior to anteriormost tip of Pb3.

LI2 on posterolateral edge of Pb3 somewhat medial to medial end of Eb3.

TD comprises TPb2, TPb2a, TEb2, and TPb3-Eb4. CT covers entire dorsal surface of anterior TD components. TPb2 in two essentially separate parts, possibly the result of LI1's passing between parts; anterior part bilobed with mid-longitudinal raphe separating lobes and attaching dorsally to CT cover; muscle attaches to anterolateral cartilaginous tip of edentate Pb2; muscle forms shallow, posteriorly opening pocket into which anterior fourth of Pb2 inserts. Posterior portion of TPb2 arises medially from broad CT band extending across dorsally naked Pb3 articulating facets; muscle extends anterolaterally and inserts on dorsolateral edge of Pb2. TEb2 very reduced, may be present bi- or unilaterally or totally absent (absent in the two juveniles and in ②); muscle arises from CT at posterolateral end of posterior section of TPb2 extends short distance and attaches to posteromedialmost edge of Eb2. TPb2a with mid-longitudinal raphe, smaller than and mostly ventroposterior to TPb2, attaches to ventroanterolateral edge of Pb2, covering most of Pb2 ventral surface extending posterior to TPb2 pocket (N.B., although muscle is posterior to TPb2, it appears that Pb2 has rotated dorsoposteriorly in effecting its more lateral attachment with Eb2; without rotation, the muscle would be on the anterior surface of Pb2, similar to that of atherinomorphs and the labrid *Achoerodus*). TPb3-Eb4 attaches to dorsomedian surface of Pb3, continuing laterally past attachment to Pb3 and attaching on expanded posteromedial surface of Eb4.

OD3-4 originates broadly from dorsoposterior surface of Pb3 and inserts on both Eb3 and Eb4 at joint formed with Eb3 uncinat process, and along Eb4 surface posteromedial to this joint.

OP origin on posterior surface of Eb4 along line just below insertion line of LP (q.v.), insertion on distal end of Cb5 dorsally.

CPb complex, apparently derived from SO longitudinal fibers with which it is continuous posteriorly; mainly comprises anterior cylindrical portion (no anteromedian raphe) that curves around anterior and lateral margins of both Pb3s. Cylindrical portion fibers almost vanish at posterolateral corner of each Pb3, but, on each side, a few fibers curve medially and become confluent with broad, strong group of fibers that attach posteromedially to Pb3. The latter fibers curve medially, passing anteriorly between the Pb3s and ventral to dorsal fibers that are continuous posteriorly with the SO longitudinal fibers. The anteriorly passing fibers branch right and left anteriorly and continue on their respective side as slips of muscle ventral to the ventroanterior surface of Pb3. The muscle slips become confluent with the anterior inner margin of the cylindrical portion of CPb.

Ad1-3 present, each attaches along anterolateral surface of its respective Eb and anterodistal surface of its respective Cb.

Ad4 (not illustrated) on ventroanterior surface of Eb4 and dorsal surface of Cb4 just medial to inner angle formed by Eb4-Cb4 joint; not visible in dorsal view, obscured by OP in posterior view.

Ad5 vertically elongate, on posterodistal ends of Cb4 and Cb5; in small specimens of both species Ad5 not clearly separable from OP and a few fibers of Ad5 attach to distal end of Eb4.

SOD absent.

RDs moderately separated, vertically short, each consisting of a partially round (in vertical cross section) anterior section that is continuous posteriorly with a horizontally longer, obliquely posteriorly directed section; band-like tendon incorporated as ventral surface of each RD, which inserts on medial surface of Pb3.

Additional remarks. SCL fine, free from posterior end of Bb3, which is not elongate. TV4 bipartite, attaches anteriorly on each side of median ventral keel of Cb5. Pb4 and UP4 absent. Pb2 edentate. IAC absent. Eb4 levator process absent.

Acanthuroidei

LUVARIDAE

Luvarus imperialis Rafinesque, MCZ 55003, 156 mm.

Plate 170

Description.

LE1 short, on cartilaginous tip of Eb1 uncinat process.

LE2 dorsally on posteromedial edge of Eb2.

LE3 tendinously on joined cartilaginous tips of Eb3 and Eb4 uncinat processes, attachment more on Eb3 than Eb4; additionally, a long slender ligament attaches cartilaginous tip of Eb3 uncinat process to cranium.

LE4 mostly destroyed, along with LP, in dissection; remainder on Eb4 dorsoposterior edge distal to uncinat process, connected by raphe with dorsolateral edge of OP, such that release of raphe from Eb4 produces a "sling"; attached to, but easily separated from, medial surface of broad membrane (not illustrated) that passes lateral to other levators and extends posteriorly and includes LP and PP (see following remarks).

Remarks. Winterbottom (1993a:29) described LE4 and LP in acanthuroids:

"In all the acanthuroids examined, the fourth levator externus not only inserts on the dorsal rim of epibranchial 4, but continues posterior to this into the dorsomedial wall of the branchial chamber (Fig. 11). In siganids and *Luvarus*, a levator posterior arises from the region of the prootic/pteric junction and joins the posterior fibers of levator externus IV in the wall of the branchial chamber (Fig. 11). Posterolaterally, the protractor pectoralis arises from the ventrolateral tip of the pterotic and passes ventrally to the posterior wall of the branchial chamber and the

anterolateral face of the cleithrum. All of these muscles are represented by thin sheets of muscle fibers. In *Zanclus*, the protractor pectoralis is joined medially by a fan-shaped sheet of fibers from the ventrolateral prootic (= levator posterior?) . . . In acanthuroids (Fig. 12), the fibers to the medial wall of the branchial chamber are separated by connective tissue from those of the protractor pectoralis. Occasionally, some fibers are present in this connective tissue in a position where one might expect a levator posterior to be (e.g., *Acanthurus triostegus*), but this is not the case in the majority of the acanthuroids dissected."

LP destroyed during dissection. See remarks following LE4 above.

LI1 on Pb2 dorsoanteriorly.

LI2 on Pb3 cartilaginous posterior end dorsoanteriorly, opposite anteromedial end of Eb3.

TD comprises TEb2, TPb3, and TEb4. TEb2, in three parts: one in middle and one on each side linked by thick CT pad; middle part small, triangular; lateral parts strap-like, medially joining lateral edges of CT pad and laterally extending onto Eb2 dorsally lateral to LE2 insertion. TPb3 joins medial margins of Pb3s ventral to OD3s. TEb4 a slender strap joining Eb4s just ventromedial to uncinat processes.

Remarks. Winterbottom (1993a:30) stated that *Luvarus* is unique among acanthuroids in lacking TD4 (= our TEb4), and possessing TD5. TEb4 in *Luvarus* is very similar to TEb4 in *Acanthurus*. We are uncertain what he meant by TD5, but this is possibly the unusually anterior SOD we recognize in *Luvarus*. Although a fine lateralmost SOD muscle filament joins OP medially, SOD can be traced to Cb5 as its ventromedial fibers fuse with OP; however, in *Acanthurus*, we also find a thin normally situated SOD that can be traced to Cb5.

OD3 origin broadly on bony dorsal surface of Pb3 ventral to TEb2, insertion on Eb3 somewhat medial to distal end continuing well up on uncinat process.

OD4 absent.

OP comprises two more-or-less distinct sections, variably almost completely separated from each other and from SOD; medial section dorsally on Pb4 posteriorly, lateral section on Eb4 dorsoposteriorly in area ventral to uncinat process, joining raphe with LE4 insertion (see OP description and remarks); both OP sections on Cb5 near posterior end.

Remarks. It is unusual for OP or SO to attach to Pb4. It is equally possible to interpret the medial OP section as SO fibers that have shifted from Eb4 to Pb4. SO attaches to Pb4 in *Polydactylus* but not in *Filimanius* (both Polynemidae).

Ad1–3 absent.

Ad4 on Eb4 posterolaterally and Cb4 narrowly posteriorly anterior to Ad5 attachment.

Ad5 very short, transverse, on Cb4 dorsoposteriorly and Cb5 dorsoposterodistally.

RDs separated by narrow space.

SOD dorsally anterior to, and free from, TEb4.

Remarks. SOD in other fishes is posterior to all TD components. See also remarks following TD above.

Additional remarks. SCL attached mid-dorsally to posteroventrally extending cartilaginous end of Bb3. TV4 free from Cb5s. Eb4 levator process absent. Pb4 and UP4 present.

EPHIPPIDAE

Chaetodipterus faber (Broussonet), USNM 289421, 74.5 mm; USNM 159268, 85.4 mm; USNM 118501, 61.3 mm.

Plate 171

Description.

LE1 broadly on Eb1 beginning lateral to uncinat process and extending almost to distal end.

LE2 broadly on Eb2 posterolaterally.

LE3 on CT joining Eb3 and Eb4 uncinat processes anteriorly (more closely associated with Eb3 than Eb4).

LE4 on Eb4 dorsally lateral to uncinat process, joining raphe with dorsal end of Ad4; Eb4 levator process absent.

LP finely tendinously on Eb4 at and lateral to LE4.

LI1 on Pb2 dorsoanteriorly, about same size as LI2.

LI2 on Pb3 dorsally opposite medial end of Eb3.

TD comprises TEb2 and TEb3-Eb4. TEb2 variably continuous musculosly transversely or broadly interrupted anteriorly by thick CT mid-section; attached dorsoanteriorly to Pb2 dorsoposteriorly by tough CT, which is continuous mid-anterioventrally with CT of pharyngeal roof; dorsomedial surface tightly covered by fascia, which gives rise to CT sheets attaching to skull; muscle extending laterally and reaching almost to dorsodistal bony end of Eb2; not continuous posteriorly with TEb3-Eb4. TEb3-Eb4 on posterior edge of Eb3 medial to uncinat process and medial edge of Eb4 ventral to tip of uncinat process, posteriorly continuous with SOD.

OD3-OD3' anteriorly on Pb3 dorsolaterally ventral to TEb2, posteriorly broadly on anterior surface of Eb3 between uncinat process and distal end, separated by shallow notch from OD3' on dorsal surface of Eb3 immediately ventral to OD3.

OD4 absent.

OP dorsally on Eb4 posteriorly beginning ventral to uncinat process and extending medially, ventrally on Cb5 dorsoposterolaterally.

Ad1-3 absent, but moderately well-developed fan-like GFM1 present (not illustrated), but GFM2 and GFM3 weakly developed.

Ad4 broadly dorsally on Eb4 posteriorly beginning ventral to uncinat process and extending laterally, ventrally broadly on Eb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Eb4 posterodistally (but not attached to AC4), ventrally on dorsoanterolateral surface of Cb5 anterior to OP.

SOD present.

RDs adjacent.

Additional remarks. SCL attached mid-dorsally to tip of ventroposteriorly extending cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. Eb4 levator process absent. Cartilage tip on Eb1 uncinat process reduced and variably absent. IAC present or absent, reduced when present, not attaching or directly impinging on Eb1 uncinat process. AC4 well-developed. Very fine Eb4 flange present. Medial end of Eb3 larger than that of Eb4.

ZANCLIDAE

Zanclus cornutus (Linnaeus), USNM 350564, 159 mm, USNM 365537, 157 mm.

Plate 172

Description.

LE1 slender tendinously on dorsoposterodistalmost edge of Eb1.

LE2 slender tendinously on dorsoposterodistalmost bony edge of Eb2, joining posterodistalmost edge of TEb2, ligament from insertion extends posteriorly and attaches to Eb3 anterolaterally.

LE3 slender tendinously on tip of Eb3 uncinat process.

LE4 and LP not separable (157 mm specimen does not exhibit diffuse separation shown by muscle fibers of illustrated specimen, which is similar on both sides), muscle sheet-like becoming fascia ventrally and attaching along lateral edges of fourth and fifth arches; PP joins fascia posteriorly.

LI1 on Pb2 dorsoanteriorly just lateral to dorsal-most cartilaginous tip.

LI2 slender tendinously on Pb3 dorsoanterolaterally medial to medial end of Eb3.

TD comprises TEb2 and TEb3-Eb4. TEb2 variable, either widely interrupted mid-dorsally by thick CT pad or continuous from one side to other; when continuous, almost inseparably attached mid-dorsally to thick CT pad (which, in either type TEb2, attaches tightly ventrally to Pb2 and Pb3 and is tightly attached dorsally to thin mid-ventral process of parasphenoid), with small muscle remnant attaching mid-posteriorly on CT pad; muscle of both types extends laterally and attaches along most of dorsal surface of Eb2. TEb3-Eb4 of two continuous sections, anterior section triangular, with mid-longitudinal raphe, apex anterior, attaches to CT between Pb3s; posterior section, broad attaches mainly to dorsomedial edge of Eb4 near articulation with Eb3 uncinat process and secondarily tendinously to medial edge of Eb3 just ventral to tip of uncinat process, continuous posteriorly by diagonal muscle strands with SOD.

OD3 origin mostly ventral to TEb2, but small branch (not illustrated) extends anteroventrally and attaches on dorsolateral surface of Pb2, main portion attaches to CT pad attached to dorsolateral surface of Pb3, insertion on dorsolateral surface of Eb3.

OD4 absent.

OP slender, dorsally on Eb4 posteriorly joining TEb3-Eb4 ventrolaterally, ventrally on Cb5 just posteromedial to Ad5.

Ad1–3 absent, but weak GFM's present on anterior surfaces of relevant Eb-Cb joints of first three arches and, unusual for fishes, on anterolateral surface of Eb4.

Ad4 dorsally on Eb4 posterolaterally beginning ventral to margin articulating with Eb3 uncinat process and extending laterally to near end of bony surface, ventrally, narrowly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally narrowly on Cb4 posterodistally, ventrally narrowly on Cb5 dorsodistally anterior to OP.

SOD present.

RDs relatively small, slightly separated.

Additional remarks. SCL attached mid-dorsally to autogenous cartilage, which is attached to ventroposterior cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed.

ACANTHURIDAE

Acanthurus nigrofuscus (Forsskål), USNM 338195,
3 specimens, 101–104 mm.

Plate 173

Description.

LE1 finely tendinously and muscoulously (tendon borders muscle anteriorly) on dorsoposterodistalmost edge of Eb1.

LE2 finely tendinously and muscoulously (tendon borders muscle anteriorly) on dorsoposteriorly expanded surface Eb2 laterally.

LE3 finely tendinously and muscoulously (tendon borders muscle anteriorly) on tip of Eb3 and Eb4 uncinat processes, mainly on Eb3.

LE4 and LP not separable (if both are present), muscles sheet-like, becoming broad CT sheet ventrally and attaching along lateral edges of fourth and fifth arches; various tendinous extensions of the CT sheet attach to other skeletal elements; fine tendon extends from LE4+?LP ventroanteriorly and inserts on Eb4 lateral to uncinat process (possibly indicating LE4 insertion); CT sheet joined posteriorly by PP. See also remarks following LE4 in *Luvarus*.

LI1 on Pb2 dorsoanteriorly ventral to dorsalmost tip of Pb2.

LI2 on Pb3.

TD complex comprising TEb2, TEb4, and TD plexus. TD plexus comprises three slender muscles

(easily removed during dissection) originating from dorsoposterolateral edge of CT pad; anterior muscle extends anterolaterally passing dorsal to TEb2 and inserts on posterodistalmost cartilaginous edge of Eb1 at LE1 insertion; middle muscle extends laterally and slightly anteriorly and inserts finely, tendinously on posterior edge of Eb2 just posterior to LE2 insertion; posterior muscle extends laterally and slightly posteriorly, and inserts on Eb4 uncinat process. TEb2 broad, originates on CT pad just anterior to TD plexus, fans out laterally, and attaches on most of bony dorsal surface of Eb2. TEb4 uninterrupted, inserts on Eb4 posteriorly just medial to uncinat process, finely continuous posteriorly with SOD.

OD3 originates on lateral edge of Pb3 and inserts on most of bony dorsal surface of Eb3.

OD4 absent.

OP dorsally mostly on Eb4 posteroventrally, but meeting TEb4 dorsolaterally; ventrally on Cb5 dorsally.

GFM1–3 fine splay of muscle fibers on anterior surface of Eb-Cb joints (weakest on Eb3-Cb3), attaching laterally to gill filaments.

Ad4 dorsally on Eb4 posteriorly beginning ventral to uncinat process and extending laterally, ventrally narrowly tendinously on Cb4 posterolaterally.

Ad5 on Cb4 posterodistal end and AC posterolaterally, joining raphe dorsoanteriorly with OP ventrolaterally; debatable if Ad5 joins CT attaching AC to Cb4.

SOD slender.

RDs slender, proximate posteriorly, separated by distance less than one RD diameter anteriorly.

Additional remarks. SCL attached mid-dorsally to autogenous cartilage, which is attached to elongate posteroventral cartilaginous end of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb2 toothed. IAC absent. Relatively large AC4 attached to dorsodistalmost surface of Cb4 and posterodistalmost surface of Eb4. IAC absent. Eb4 levator process absent.

Anabantomorpha

Britz (2003) briefly recapped the classificatory history of the suborder Anabantoidei, in which he recognized three families (Anabantidae, Helostomatidae, Osphronemidae), which have well-developed supra-branchial organs. He stated that the closest relatives of the group appear to be the Channidae, which have a much lesser-developed supra-branchial organ, and that the four families, together with Badidae, *Nandus* (family not indicated, but Nandidae is available), and *Pristolepis* (family not indicated, but Pristolepidae is available) form a monophyletic group based on the synapomorphic presence of parasphenoid teeth. To recognize the monophyly of this group of families, we erect a new ordinal-group name **Anabantomor-**

pha, retaining Anabantoidei for the four families with suprabranchial organs (note: we did not examine any heleostomid or osphronemid gill arches).

NANDIDAE

Nandus nebulosus (Gray), USNM 328105, 49.3 mm.

Not illustrated

Description.

LE1 on Eb1 dorsoposteriorly a little lateral to articulation with IAC (no uncinat process, IAC very long, articulates directly with bone of Eb1; like *Pristolepis*, Plate 174).

LE2 on bony prominence on Eb2 mid-dorsoposteriorly.

LE3 finely, tendinously on tip of Eb3 uncinat process.

Remarks. Liem (1970:56–57) stated (and illustrated) that only three LEs are present in the nandids he examined (included *N. nandus* and *N. nebulosus*). There is a possibility that he either overlooked the fine LE3 we observed, or that there is variation in its occurrence.

LE4 largest levator, on bony surface of Eb4 just anterior to cartilage tip of levator process.

LP on Eb4 posterolaterally beginning medially at lateral edge of LE4 insertion and extending laterally.

LI1 on dorsoanteriormost cartilaginous tip of Pb2 at joint with IAC.

LI2 on Pb3 dorsolaterally with main portion of insertion continuing onto UP4 dorsally ventral to medial end of Eb3.

TD comprises TEb2, TPb3-Eb3-Eb4. TEb2, well developed, uninterrupted (musculous medially), with mid-longitudinal raphe; muscle extending laterally and attaching on Eb2 dorsally anterior to LE2 insertion (dorsal surfaces of Pb3s covered by muscle). TPb3-Eb3-Eb4 on Pb3 beginning anteromedial to medial end of Eb3, continuing posteriorly on cartilaginous posteromedial end of Eb3, and then onto anterior and posterior bony edges of Eb4 medial to bony support of uncinat process.

OD3–4 originating on Pb3 dorsomedially and inserting on Eb3 anterior surface ventral to tip of uncinat process and on Eb4 dorsally just lateral to tip of uncinat process.

OP strap-like; dorsally on Eb4 ventroposteriorly beginning about mid-way between medial end and levator process and extending laterally almost to levator process, posteriorly overlapping dorsomedial edge of Ad4; ventrally on Cb5 dorsally, beginning immediately medial to cartilaginous posterior tip and extending a short distance medially and meeting posterolateral edge of TV5.

Ad1–3 weakly developed, spanning respective Eb-Cb joint anteriorly posterior to gill rakers; easily overlooked.

Ad4 dorsally on Eb4 ventroposteriorly, beginning a little ventromedial to levator process (and anterior to OP laterally) and extending laterally most of bony length of Eb4; ventrally on Cb4 dorsally beginning a little medial to Eb4-Cb4 joint and extending medially a short distance.

Ad5 anteriorly on posterodistalmost surface of Cb4; posteriorly on posterodistal surface of Cb5, meeting OP.

SOD absent.

RDs well separated at origins, gradually converging and becoming adjacent at insertions on Pb3s medially and UP4s dorsomedially.

Additional remarks. SCL free from posterior end of Bb3. TV4 free from Cb5s. Pb4 absent. UP4 present. IAC very long. Pb1 present, bony, with dorsal and ventral cartilaginous caps. Eb4 with small bony flange dorsoanterodistally. Pb2 toothed.

See Interrelationships section following additional remarks in description of *Badis kyar* (Badidae) for comments on other characters of anabantomorphs.

BADIDAE

Badis kyar Kullander and Britz, USNM 343545, 39.1 mm.

Not illustrated

Description.

LE1 on Eb1 mid-dorsoposteriorly.

LE2 insertion begins on Eb2 mid-dorsoposteriorly and continues onto Eb3 mid-dorsoanteriorly.

LE3 on Eb3 just ventral to tip of uncinat process.

LE4 on Eb4 dorsally posterior to all bony uncinat process, meeting LP insertion anteriorly. Insertion is dorsal to minute cartilage tip of levator process on one side, cartilage tip absent on other side.

LP on Eb4 at and posterior to LE4 insertion, fibers continuous posteriorly with Ad4 dorsoposterolaterally.

LI1 on dorsoanteriormost cartilaginous tip of Pb2 at joint with IAC.

LI2 on Pb3.

TD comprises an undivided TEb2 (which is only weakly developed as it passes over the Pb3s dorsally) and attaches on Eb2 anterior to LE2 insertion, and TPb3-Eb4. Most of the dorsal surface of Pb3s not covered by muscle.

OD3–4 origin on Pb3 dorsomedially ventral to TEb2; insertion on Eb3 dorsoanteriorly just ventral to tip of uncinat process and on Eb4 dorsoposteriorly just ventral to tip of uncinat process; separate (anomalous?), small posterior section originates on Pb3 dorsomedially immediately posterior to other (usual) OD3–4 origin, extends laterally, and curves a little as it extends to its attachment on Eb4 just medial to dorsomedial edge of OP.

OP present, strap-like, dorsally on Eb4 ventrally

ventral to LP insertion, ventrally on Cb5 dorsally near distal end, there meeting Ad5 posteriorly.

Ad1–3 very well developed, probably relatively larger than in any other acanthomorph taxon we examined, broadly spanning respective Eb–Cb joint.

Ad4 dorsally on Eb4 ventrally beginning anterior to OP laterally and extending to Eb4–Cb4 joint, continuous dorsoposterolaterally with LP posteroventrally; ventrally on Cb4 extending medially from Eb4–Cb4 joint.

Ad5 attaches distal end of Cb5 to distal end of Cb4.

SOD absent.

RDs relatively massive, juxtaposed.

Additional remarks. SCL apparently free from Bb3. TV4 free from Cb5s. IAC similar to that of *Nandus* in relative length and in joining only the bone of Eb1 (uncinate process absent in both taxa). Pb1 is entirely cartilaginous (mostly bony in *Nandus*). Pb4 absent. UP4 present. Eb4 with small bony flange dorsoanterodistally. Pb1 cartilaginous. Pb2 toothed.

Interrelationships. Kullander and Britz (2002:300) hypothesized a monophyletic group comprising Badidae and Nandidae (latter including only *Nandus*) based primarily on the shared presence of a deeply bifurcated hemal spine on vertebra PU2, which occurs in no other teleost [we found a deeply bifurcated HPU2 in two of three radiographed specimens of *Scatophagus argus*, USNM 259383, but not in five cleared and stained specimens, USNM 197528, 224393]. Kullander and Britz offered as additional evidence for monophyly, the presence of 7+7 principal caudal-fin rays, compared with 8+8 in Polycentridae and Pristolepidae, various members of which have been considered by authors as related to the nandids.

In addition to those characters reported by Kullander and Britz, we find that our specimens of Badidae and Nandidae are unusual in having the IAC articulating directly with the bony surface of Eb1, which lacks a cartilage-tipped Eb1 uncinate process. A similar condition is found in the probably closely related *Pristolepis* (Pristolepidae). A somewhat similar condition also exists in the synbranchiform Synbranchidae, in which there is an IAB (purportedly an ossified IAC; Rosen and Greenwood, 1976). The synbranchid IAB articulates directly with the bony surface of Eb1, which lacks a cartilage tipped uncinate process. The condition in certain atherinomorphs (aplocheilids, cyprinodontids), in which an Eb1 uncinate process appears to be absent and IAC articulates with the distal, cartilaginous end of Eb1, is also dissimilar to the condition in Badidae and Nandidae.

Nandids and badids share in having another specialization, presence of a bony flange, or spur, overlapping cartilaginous distal end of Eb4. Although

limited to and common among percomorphs, the Eb4 flange occurs otherwise in anabantomorphs only in anabantids, osphronemids (*Luciocephalus*, Britz, 1995:fig. 4; *Macropodus*, *Betta*, Britz, 2001:figs. 2b, c; flanges not labelled in any of Britz's figures, but presence clearly indicated), and probably heleostomatids (not examined by us). The flange is not present in pristolepids and the channids we examined.

PRISTOLEPIDAE

Pristolepis fasciata (Bleeker), USNM 103105, 68 mm.

Plate 174

Description.

LE1 slender, tendinously on Eb1 dorsoposteriorly a little lateral to articulation with IAC (no uncinate process; IAC articulates directly with bone, as it does in *Nandus* and *Badis*), left side with muscle fibers extending along entire medial edge of incorporated tendon; muscle attaching only to distal end of slender tendon on right side.

LE2 slender, mostly tendinously on slight bony prominence on dorsoposterior edge of Eb2.

LE3 finely tendinously on tip of Eb3 uncinate process, tendon partly joining OD3–4 (muscle also present on both sides of a partially dissected specimen).

Remarks. Liem (1970:56–57) stated that only three LEs are present in the anabantomorphs he examined (included *P. fasciata*). There is a possibility that he either overlooked the fine LE3 we observed, or that there is variation in its occurrence.

LE4 largest levator, tendinously on dorsodistalmost bony edge of Eb4 levator process.

LP tendinously at and anterior to LE4 insertion, extending onto dorsodistalmost end of levator process.

LI1 on dorsoanteriormost cartilaginous tip of Pb2 at joint with IAC.

LI2 tendinously on dorsoposterolateral surface of Pb3 near junction with Pb4 and medial end of medial end of Eb3.

TD comprises TEb2 and TEb4. TEb2 comprises a muscle pair, each member of which is joined to lateral edge of broad, very thick CT pad, which attaches ventroanteromedially to Pb2; posteroventral half of pad is free, overlies and is continuous anteroventrolaterally with bilateral pair of thinner CT pads, each of which covers dorsal bony surface of its respective Pb3 and is attached to dorsomedial edge of Pb3; ventral pad is joined laterally by OD3–4 origin; muscle extends laterally and attaches on Eb2 dorsally anterior, or slightly anterolateral, to LE2 insertion. TEb4 attaches on Eb4 posteromedially.

OD3–4 origin on lateral edge of CT pad covering Pb3 dorsally and on dorsoanterior bony surface of Pb3, insertion on medial edge and anterior surface of

Eb3 uncinat process and medial edge and anterior surface of Eb4 uncinat process.

OP dorsally on posterior surface of Eb4, extending laterally from uncinat to levator process, ventrally on Cb5, ventrolaterally penetrated by raphe, medially continuous with SO.

GFM1–3, that on first arch very weakly developed, all three just reaching to anterodistalmost end of respective Cb.

Ad4 dorsally on posterolateral surface of Eb4, ventrally on dorsal Cb4 surface anterior to Eb4-Cb4 joint.

Ad5 dorsally tendinously on posterolateral surface of Eb4 and ventrally on dorsodistalmost end of Cb5, joining raphe anteroventrolaterally with OP.

SOD absent.

RDs separate, insert on Pb3 and UP4 posteriorly.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Pb4 absent. UP4 present. Pb1 bony with cartilaginous ends. Pb2 toothed.

See Interrelationships section following additional remarks in description of *Badis kyar* (Badidae) for comments about the relationships of Nandidae, Badidae, Pristolepidae, Channidae and Anabantoidae.

CHANNIDAE

Channa asiatica (Linnaeus), USNM 191304, 117 mm; USNM 192925. 98.0 mm.

Plate 175

Additional material. *Channa harcourtbutleri* (Annan-dale), USNM 191465, 90.4 mm.

Description.

LE1 on posterior edge of broadly expanded Eb1 a little lateral to mid-length (uncinat process absent).

LE2 slender, on tip of bony process at distal end of Eb2.

Remarks. Insertion of LE2 at the distal end of Eb2 is uncommon in acanthomorphs. It also occurs in some gobioids and atherinomorphs as a specialized state within these groups. It also appears to be a specialized state within anabantomorphs. That TEb2 fails to reach the LE2 insertion in *Channa* is probably the result of the extreme lateral shift in position of the LE2 insertion, not of a reduction in the lateral extent of TEb2.

LE3 slender, on tip of Eb3 uncinat process.

LE4 slender, tendinously on Eb4 dorsally at about mid-anterior point of LP insertion, closely applied posteriorly to anterior surface of LP and difficult to distinguish from LP.

LP massive, broadly dorsally on most of distalmost half of Eb4, joining extensive raphe posteriorly with OP dorsally.

Remarks. The angle of direction from insertion to origin is the same as that of LE4. In most acantho-

morphs the LP angle diverges noticeably from that of LE4. LP normally inclines posteriorly or posteromedially from LE4.

LI1 on Pb3 dorsoanteromedially (note: Pb2 well developed; positioned ventral to anterior portion of Eb2, relatively well-separated from Pb3); insertion heavily enveloped in CT involving medial end of Eb2 and ventral surface of thick CT area joining TEb2 with contralateral TEb2.

LI2 on Pb3 dorsoposteriorly.

TD comprises TEb2 and TPb3-Eb4. TEb2 a pair of muscles joined by broad area of tough, thick, layered CT, which is notched anteriorly as it passes around the parasphenoid tooth patch, and gives rise to CT sheet attaching to skull, muscle fibers essentially cover Pb3 dorsal surface, but are separated from it by thick CT layer; muscle attaching to a little more than medial half of posterior edge of Eb2, failing to reach the insertion of LE2 (see remarks following LE2), not continuous posteriorly with TPb3-Eb4. TPb3-Eb4 narrowly on Pb3 dorsoposteromedially, continuing more broadly posteriorly and attaching on Eb4 posteromedially.

CPb (not illustrated) a slender extension of the SO longitudinal muscle layer jointly encircling Pb3 and UP4, with an even more slender muscle filament passing between Pb3 and UP4 and connecting both sides of the encircling portion of the muscle.

OD3–4 origin dorsally from margin of large centrally, located CT sheet, ventrally from Pb3 dorsally just lateral to dorsomedial surface; minor insertion on Eb3 uncinat process anteriorly, main insertion on Eb4 beginning on anterior surface just posterior to Eb3 uncinat process, and continuing laterally on narrow dorsal surface to medial edge of LP.

OP dorsally variably broadly on Eb4 posteriorly, meeting OD3–4 and LP; always most distinct ventrolaterally with fibers attaching to tendinous sheet coursing along ventrolateral surface of muscle and conforming with Ad5 dorsally; ventrally OP meets PCI but does not join raphe with it; medial edge of OP weakly to well separated from SO.

Ad1 absent.

Ad2 bulky muscle dorsally on Eb2-Cb2 joint anteriorly, extending short distance ventrally on Cb2.

Ad3 dorsally on much of anterior edge of Eb3, but ceasing a little medial to distal end, there a short, separate portion present dorsally, both portions attaching ventrally to anterior surface of Cb3 slightly ventral to Eb3-Cb3 joint.

Ad4 dorsally on most of Eb4 ventrally, continuing laterally to end of inner angle of Eb4-Cb4 joint, ventrally on most of Cb4 dorsally (not visible externally).

Ad5 dorsally on posterodistal surfaces of Eb4 and Cb4, ventrally on Cb5 posterodistally; with fine raphe-like inclusion on surface (both sides) only in

larger specimen (illustrated); joins raphe with PCI near distal end of Cb5. ② Dorsally only on Cb4 distally.

SOD absent.

RDs separated by space less than half one RD diameter.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Pb1 bony with ventral end cartilaginous. Pb2 finely toothed. Pb4 absent, UP4 present. Eb4 uncinatate and levator processes absent. IAC absent.

ANABANTIDAE

Sandelia bainsii Castelnau, USNM 363314, 83.7 mm.

Not illustrated

Additional material. *Ctenopoma kingsleyae* Günther, USNM 288037, 54.1 mm. The muscles appear to be essentially the same as those of *Sandelia*.

Description.

LE1 slender, short, on posterior edge of broadly expanded Eb1 mid-dorsoposteriorly.

Remarks. Right-side Eb1 has a fine, cartilage tipped uncinatate process joining a very slender IAC, which becomes finely ligamentous medially. It is unclear what the ligament attaches to; it was broken during dissection, but was probably attached to the tip of long dorsal process of Pb2. Eb1 uncinatate process and IAC are absent on left side.

LE2 slender, short, on raised bony prominence on Eb2 mid-posteriorly.

LE3 on tip of Eb3 uncinatate process anteriorly.

LE4 robust, on Eb4 dorsolaterally, fused posteroventrally with LP, but the two muscles have slightly separate origins.

Remarks. The bony dorsal surface of Eb4 extends laterally as a shelf (flange), the ventral surface of which attaches to the somewhat elongate dorsal cartilaginous distal end of Cb4. On one side, just medial to the attachment of Cb4 to Eb4, is an alcian-blue stained area, which probably represents a vestige of a former (present early in ontogeny?) distal cartilaginous end of Eb4. The area is absent on the other side. Eb4 and the joint with Cb4 are closely reminiscent of the structures in cichlids, except that cichlids retain the cartilaginous distal end of Eb4. Also in cichlids, LE4 fuses posteroventrally with LP.

LP fusing ventroanteriorly with LE4 and inserting together on Eb4 dorsolaterally.

LI1 inserts by slender tendon on Pb3 dorsoanterolaterally.

LI2 inserts by short tendinous strap on Pb3 anterolaterally, a little medial to articulation with medial end of Eb3.

TD comprises only TPb2 and TPb3. TPb2 joins lateral margin of CT pad covering otherwise naked

Pb3 dorsal facet; muscle is small, sheet-like, and almost vertical, extending laterally and attaching to Pb2 along medial edge and surface of long, dorso-medially extending Pb2 uncinatate process. TPb3 attaches broadly to posteromedial margins of Pb3s.

CPb extends as a broad continuation of SO longitudinal muscle between pharyngobranchials, dividing and becoming string-like anteriorly and extending around periphery of Pbs on each side, but with short medial branch attaching to posterolateral corner of Pb2, and posteromedially re-joining SO.

OD3–4 relatively large, most prominent muscle; anteriorly, broadly on Pb3 dorsomedially, posteriorly on Eb3 uncinatate process dorsoanteriorly and on all bony Eb4 uncinatate process dorsally.

OP dorsally on Eb4 ventrally beginning medially well medial to LE4-LP insertions and extending laterally to about mid-way below insertions, ventrally on Cb5 dorsoposterolaterally, meeting but not joining raphe with PCI and joining raphe with Ad5 ventromedially.

Ad1–3 absent. GFM1 a thin muscle extending along posterior edge of Eb1 from near LE1 insertion to Eb1-Cb1 joint. GFM2 with small attachment to Eb1 posteriorly well lateral to LE1 insertion, with main portion of muscle on anterolateral edge of Eb2, reaching to Eb2-Cb2 joint. GFM3 well developed, on Eb3 dorsally with small attachment to Eb2 posteriorly. These muscles do not span the anterior surfaces of the Eb-Cb joint.

Ad4 dorsally, broadly on Eb4 ventrally beginning medially anterior to OP and ventral to LE4-LP insertions and extending laterally to near distal end; ventrally on Cb4 dorsally, narrowly on distalmost bony surface.

Ad5 dorsally on Eb4 ventrally at distalmost surface, ventrally on Cb5 dorsodistally, joining raphe with OP ventromedially.

SOD absent.

RDs adjacent.

Additional remarks. SCL present. TV4 free from Cb5s. Pb4 absent. UP4 present. Pb1 bony with cartilage ends. Pb2 finely toothed; teeth absent in *Ctenopoma*. Eb4 levator process absent. Medial end of Eb4 much larger than medial end of Eb3.

See Interrelationships section following additional remarks in description of *Badis kyar* (Badidae) for comments about the relationships of Nandidae, Badidae, Pristolepidae, Channidae and Anabantidae.

Stromateoidei

Ever since Haedrich's (1969) original description of *Amarsipus* and consideration of it as an aberrant stromateoid, *Amarsipus* has been considered to be a stromateoid. Although there is a general external similarity of *Amarsipus* to the "true" stromateoids (taxa

sharing the specialization of having a toothed sacular outgrowth of the gut posterior to fourth gill arch), a close relationship between the two groups has not been hypothesized cladistically. *Amarsipus* lacks the sacular outgrowth, and, therefore, that character cannot be used to relate it to the stromateoids. The other characters used by Haedrich (1967) to define the Stromateoidei (for list, see interrelationships discussion of the Icosteidae, which has also been considered to be closely related to the stromateoids), are either generalized or inexplicit, with the possible exception of their possessing "an extensive subdermal canal system," a character that, to our knowledge, has not been surveyed.

Freihofer (1973:table 1, p. 138) reported that stromateoids have the highly specialized pattern 10 of the orbito-pectoral branch of the ramus lateralis accessorius (RLA-OP). Only in pattern 10 does the RLA-OP pass posteriorly beneath the skin paralleling the pterotic canal, then pass between the dorsal end of the preopercular canal and posterior end of the pterotic, continue beneath the skin overlying the levator opercularis muscle, and then extend medially around the joint between the post-temporal and supracleithrum onto the medial side of the pectoral girdle. We checked the posterior extension of RLA-OP in the stromateoid *Peprilus burti* (USNM uncataloged, field no. U60-7), beginning in the region near the dorsal end of the preopercular canal and corroborate Freihofer's observations. We also dissected a specimen of *Amarsipus* (SI0 61-547), beginning in the region near the dorsal end of the preopercle to determine the position of its RLA-OP. RLA-OP in *Amarsipus* appears to parallel the pterotic, but it does not pass below the surface of the skin nor does it approach the post-temporal-supracleithrum joint. Rather, it passes medial to the thick mass of opercular muscles and extends posteriorly well ventral to the post-temporal-supracleithrum joint as it enters the medial side of the pectoral girdle. Inasmuch as we were unable to completely trace RLA-OP from its origin, we cannot say which, if any, of Freihofer's RLA-OP patterns pertains to *Amarsipus*, but it is certainly not pattern 10 as he described it. This finding does not necessarily provide evidence that *Amarsipus* is not closely related to the stromateoids (see also Inter-relationships discussion following description of *Icosteus*, Icosteidae), but it does suggest that more study is necessary before it can be "concluded" that *Amarsipus* and stromateoids are closely related.

Johnson and Fritsche (1989) included the stromateoids together with a group of families that we have segregated in the Girelloidei. They based their group primarily on the fact that all shared Freihofer's RLA pattern 10. Johnson and Fritsche did not examine *Amarsipus*. If *Amarsipus* is a stromateoid (sister group to all other stromateoids), more evidence will

be necessary in order to relate the stromateoids to the girelloids.

Our inclusion of the monotypic Amarsipidae in the Stromateoidei is provisional.

AMARSIPIDAE

Amarsipus carlsbergi Haedrich, SIO-75-116, 44.0 mm.

Plate 176

Description.

LE1 on dorsal edge of Eb1 at and just lateral to tip of uncinat process.

LE2 on raised dorsoposterior edge of Eb2.

LE3 very slender, on dorsoanterior edge of Eb3 uncinat process.

LE4 on Eb4 just lateral to cartilage tip of uncinat process (no levator process).

LP on Eb4 at distal edge of LE4 insertion.

LI1 on anteromedial surface of Pb2 medial to IAC attachment.

LI2 on Pb3 dorsolaterally.

TD comprises TPb2, TEb2, and TPb3-Pb4. TPb2 thin, heart-shaped (notched anteriorly) with mid-longitudinal raphe, attached anterolaterally to anterior tip of Pb2, broadly continuous ventrally with TEb2. TEb2 with (unusual) slight but definite tendinous attachment to anterior tip of Pb2 at junction of LI1 insertion and with anterolaterally and posterolaterally extending fibers joining at about medial end of Eb2 and attaching on dorsal surface of Eb2 anterior to LE2 insertion; posteriorly free from TPb3-Pb4. Fibers from TPb3-Pb4 extending anteriorly ventral to TEb2 and attaching to Pb3s anteromedially, posteriorly attaching to dorsoposterior surface of Pb3 and dorsal surface of Pb4, continuous posteriorly with SOD.

OD3-4, OD3' origin on Pb3 dorsolaterally ventral to TEb2, inserting on dorsoanterior surface of Eb3 uncinat process and dorsoanterior surface and dorsomedial edge of Eb4, forming ventrolateral branch, OD3', slightly distal to mid-length, and inserting on Eb3 dorsoanterior surface just ventral to OD3-4 insertion.

OP dorsally on Eb4 posterior surface at and medial to uncinat process, ventrally on posterodistal surface of Cb5, posterior to Ad5 attachment.

Ad1-3 absent.

Ad4 dorsally on ventral surface of Eb4 lateral to uncinat process, ventrally on Cb4 dorsally anterior to Eb4-Cb4 joint.

Ad5 ventrally on Cb5 dorsodistal surface, dorsally on Cb4 distal end.

SOD present.

RDs separate.

Additional remarks. SCL appears to be free from Bb3 (needs verification in another specimen). TV4

free from Cb5s. See Icosteidae for discussion of *Amarsipus* interrelationships. Pb4 and UP4 present. Pb2 toothed.

CENTROLOPHIDAE

Psenopsis sp., USNM 304398, two specimens, 80.5–90.0 mm.

Plate 177

Description.

LE1 on dorsal edge of Eb1 uncinat process just lateral to cartilage tip.

LE2 on mid-dorsoposterior edge of Eb2.

LE3 on tip of Eb3 uncinat process.

LE4 on dorsoanterior surface of Eb4 levator process.

LP on Eb4 levator process just anterior to LE4 insertion.

LI1 tendinously on dorsoanterolateralmost surface of Pb2 just medial to joint with IAC.

LI2 on Pb3 dorsoposteriorly and dorsoanterolateral edge of Pb4, meeting posterolateral edge of TPb3-Pb4-Eb3.

TD comprises TPb2, TEb2, and TPb3-Pb4-Eb4. TPb2 an almost circular ribbon of muscle interrupted anteriorly where it ventrally joins CT of pharyngeal roof and dorsally joins CT sheet covering muscle and attaching to skull; muscle attaching anteroventrolaterally to joined cartilaginous dorsoanterior ends of Pb2 and Pb3, posteriorly fusing with TEb2 and posterior continuation of pharyngeal roof CT, which tightly covers musculously naked Pb3 dorsal facets (TEb2 muscle fibers do not extend across central area bounded by TPb2, but in larger specimen three isolated islands of muscle are present posterior to TPb2 mid-anteriorly). TEb2 thickest anteriorly, meeting thin posterior fibers and “squeezing” as the muscle extends onto Eb2 dorsally, thick portion attaching on Eb2 dorsoanteriorly at point anterolateral to LE2 insertion, thin portion attaching to Eb2 dorsally at and anterior to LE2 insertion; muscle not continuous posteriorly with TPb3-Pb4-Eb3. TPb3-Pb4-Eb3 with fine strands of muscle attaching to Pb3 along medial edge of LI2 insertion, to bony posteromedial edge of Eb3, and to dorsal surface of Pb4 where fibers mesh with those of anterior end of M. SO-Pb4.

M. SO-Pb4 originates from SO fibers associated with lateral surface of EO and extends dorsoanteriorly and attaches to dorsal surface of Pb4 together with TPb3-Pb4-Eb3.

OD3–4 originating on Pb3 dorsoanteriorly ventral to TEb2, inserting on dorsoanterior surface of Eb3 uncinat process and anteromedialmost surface of Eb4 uncinat process.

OP apparently absent. Muscle fibers attaching to posterior surface of Eb4 levator process mesh laterally with Ad4 and ventrally with EO and M. SO-Pb4

fibers; a few fibers may extend to Cb5; situation unresolvable in specimens.

Ad1–3 absent.

Ad4 dorsally on posterodistal surface of Eb4, ventrally attaching by CT to dorsodistalmost end of Cb4; EO attaches to posterodistalmost surface of Cb4 and separates Ad4 and Ad5 attachments.

Ad5 dorsally on ventrodistalmost end of Cb4, ventrally on Cb5 distally (see also Ad4).

SOD absent.

RD posteriorly laterally compressed, slightly separated from counterpart, extends well anteriorly and attaches to anteromedial surface of Pb3.

Additional remarks. SCL attached mid-posteriorly to ventroposterior cartilaginous tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. IAC present.

Zoarcoidei

Imamura and Yabe (2002) hypothesized that the Zoarcoidei and Cottoidei comprise a monophyletic group (unnamed), which they include in the Perciformes. We found some evidence that might corroborate their hypothesis (see Additional remarks following description of *Hexagrammos stelleri*, Hexagrammidae, included under Scorpaeniformes).

BATHYMASTERIDAE

Bathymaster signatus Cope, USNM 339381, 101 mm; USNM 339378, 107 mm.

Plate 178

Description.

LE1 on medial half of Eb1 dorsally.

Remarks. Anterior arm of Eb1 interpreted as absent because the medial end of Eb1 articulates with Pb2.

LE2 on raised dorsoposterior edge of Eb2.

LE3 on dorsoanterior edge of tip of Eb3 uncinat process.

LE4 on dorsoposterior surface of Eb4 a little more than half distance to distal end, beginning above lateralmost edge of OP.

LP at and posterior to posterior edge of LE4 insertion.

LI1 in smaller specimen on Pb2 dorsoanteriorly and Pb3 anterolateralmost edge; in larger specimen on dorsolateral surface of Pb2 and anterolateral edge of Pb3.

LI2 on Pb3 at and lateral to TPb3 attachment.

TD comprises TEb2, TPb2, and TPb3-Eb3. TPb2 a laterally curving semicircular ribbon of muscle on each side arising anteriorly on each side from mid-anterior end of TEb2 and fusing at mid-posterior end; muscle not attached to Pb2. TEb2 lies dorsal to anterior ends of Pb2 and Pb3 but is free from them; its oblong dorsomedial section is notched mid-anteriorly

and mid-posteriorly, and divided mid-longitudinally by a raphe that attaches ventrally to CT of pharyngeal roof and dorsally to CT sheet that attaches to skull; laterally, TEb2 attaches along more than half length of Eb2 dorsal surface; posteriorly, TEb2 is free from, and dorsal to level of, TPb3-Eb3. TPb3-Eb3 broadly on Pb3 dorsal surface beginning along medial edge of LI2 insertion and continuing posteriorly and attaching to the very medialmost edge of Eb3, continuous posteriorly by broad, diagonal muscle strap with SOD.

OD3–4 origin on dorsomedial surface of Pb3 ventral to TEb2, insertion on anterior surface of Eb3 uncinat process, and medial edge of Eb4 uncinat process.

OP dorsally on posterior surface of Eb4, beginning slightly lateral to tip of uncinat process and extending well medially, ventrally on dorsolateral surface of Cb5, overlapping much of Ad5 posteriorly.

Ad1–3 absent (short cord-like GFM on each Eb dorsolaterally, extending onto anterodistalmost end of respective Cb).

Ad4 broadly on ventral surface of Eb4 and dorsal surface of Cb4 medial to Eb4-Cb4 joint, beginning medially a little anterior to OP.

Ad5 broadly on both dorsal surface of Cb5 and posterolateral surface of Cb4.

SOD present.

RDs separated by narrow space less than one-half diameter of one RD.

Additional remarks. SCL attached mid-dorsally to cartilaginous ventroposterior tip of Bb3. TV4 free from Cb5s. Pb4 and UP4 present. Pb1, IAC, and Eb4 levator process absent. Pb2 toothed. Medial end of Eb3 larger than that of Eb4.

ZAPRORIDAE

Zaprora silen Jordan, USNM 306369, 113 mm.

Not illustrated

Description.

LE1 tendinously on mid-dorsoposterior edge of Eb1; uncinat process absent.

LE2 narrowly tendinously on Eb2 nearer medial end than distal end, ligamentous connection from posterior base of insertion to anterior margin of Eb3.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 posterolaterally, but medial to distal end, insertion overlapped slightly by anteromedial edge of LP insertion.

LP on Eb4 beginning slightly anterior to lateral edge of LE4 insertion and extending to cartilaginous distal end Eb4.

LI1 on joined dorsoanteriormost tips of Pb2 and Pb3, slightly larger than LI2.

LI2 on Pb3 dorsally medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3-Eb3. TPb2

a bilateral pair of broadly ribbon-like semicircular muscles arising from TEb2 mid-dorsoposteriorly, curving laterally, and joining mid-longitudinal raphe, forming cup-shaped depression floored by TEb2 medially and some CT. TPb2 attaches anteroventrolaterally to anterodorsalmost tip of Pb2; mid-longitudinal raphe attaches ventrally to CT of pharyngeal roof and dorsally gives rise to CT sheets covering muscles. TEb2 extends laterally from TPb2 and attaches to Eb2 dorsally well anterolateral to LE2 insertion, meeting anteromedial end of GFM2. TPb3-Eb3 begins anterior as small, almost separate branch attaching to Pb3 anterior to LI2 insertion (same on both sides) and continues posteriorly as much broader portion, which attaches to posteromedial edge of Eb3, posteriorly continuous by diagonal muscle strands with SOD.

OD3 originates on Pb3 dorsoanteromedially and inserts on Eb3 just ventral to tip of uncinat process; on one side only, a few muscles fibers attach weakly to dorsomedialmost edge of Eb4 uncinat process.

OD4 (see OD3). We consider OD4 absent, but verification in other specimens needed.

OP dorsally on Eb4 dorsoposteriorly, beginning medial to uncinat process and extending laterally to below LE4 insertion, ventrally on Cb5 posterolaterally, overlapping Ad5 posteromedially.

Ad1–3 absent.

GFM 1 weakly fan-shaped.

GFM2 well developed, dorsomedially meeting TEb2 distally, extending laterally, weakly spanning Eb2-Cb2 joint and extending narrowly ventrally along Cb2 margin.

GFM3 similar to GFM2 (however, does not meet OD3).

Ad4 dorsally on Eb4 posterolaterally beginning below LE4 insertion and extending laterally to distal end of Eb4, ventrally on Cb4 dorsally anterior to Ad5.

Ad5 ventrally on Cb5 dorsodistally, medial edge anterior to OP, dorsally on Cb4 dorsodistally.

SOD very broad, similar to that of *Bathymaster* (Plate 178), except diagonal muscle strap passes to opposite side, and muscle slip passes through RD on one side, similar to *Nemipterus* (Plate 154).

RDs crossed and joined at origin and only briefly exposed before separating and passing ventral to SOD, but extending well anteriorly before attaching to Pb3 dorsoanteriorly, meeting OD3 attachment posteriorly.

Additional remarks. SCL free from posterior end of Bb3, which is not elongate. TV4 free from Cb5s. Pb1 absent. Pb2 toothed. Pb4 and UP4 present. IAC absent Eb4 levator process absent. Medial end of Eb3 larger than that of Eb4. PCI attaches laterally well medial to distal end of Cb5. Eb1 anterior process

absent (interpreted as such based on attachment of medial end of Eb1 to anterior tip of Pb2).

PHOLIDAE

Not examined.

Imamura and Yabe (2002:fig. 14B, 118) illustrate the dorsal gill-arch musculature of *Pholis nebulosa* (Temminck and Schlegel), but only describe Ad1–3 and a circular TPb2 (only indicated as part of TDA). LE1–4, LP, LI1–2, TEb2 attaching both anterior and posterior to LE2, OD (but not whether it attaches to both Eb3 and Eb4), TDP with attachment at least to Eb3, OP with dorsal attachment to Eb4 medial to LE4. A mid-longitudinal raphe divides TPb2 and TEb2. They also illustrate a reduced, cartilaginous Pb1 and a cartilage-tipped Eb1 uncinat process, which are the only incidences of the presence of these two elements in the zoarcoids we examined. They illustrate a ligament attaching to the cartilaginous tip of the Eb1 uncinat process and extending medially, presumably, to Pb2. *Pholis* appears to be less specialized than the stichaeid *Ulvaria*.

STICHAEIDAE

Ulvaria subbifurcata (Storer), USNM 364344, 95.4 mm.

Plate 179

Description.

LE1 on Eb1 mid-dorsoposteriorly (anterior process and Pb1 absent; uncinat process present).

Remarks. Anterior process assumed absent because medial end of Eb1 joins dorsal end of Pb2.

LE2 on Eb2 mid-dorsoposteriorly.

LE3 on anterior edge of tip of Eb3 uncinat process, meeting anteroventrally with OD3–4.

LE4 on Eb4 bony surface dorsoposterolaterally.

LP on posterolateralmost bony edge of Eb4, contiguous with posterior edge of LE4 insertion.

LI1 on dorsal surface of Pb2 and anteriormost edge of Pb3, overlying, but unattached to, medial end of Eb1 uncinat process.

LI2 on Pb3 dorsolaterally, joining raphe medially with TPb3-Eb3.

TD comprises TEb2, TPb3-Eb3, and vestigial remnant of TPb2, present only unilaterally as fine, laterally curving, semicircular muscle strand arising dorsoanteriorly from, and dorsoposteriorly re-entering, TEb2 (not connected to Pb2). TEb2 broad, with mid-longitudinal raphe, which gives rise dorsally to CT sheets covering muscles, attached mid-anteroventrally to CT of pharyngeal roof, attaching on Eb2 dorsally anterior to LE2 insertion, joining raphe with medial end of Ad2, continuous posteriorly by diagonal strand of muscle with TPb3-Eb3. TPb3-Eb3 on Pb3 dorsally joining raphe with medial edge of LI2

insertion and on posterior corner of medial end of Eb3, continuous posteriorly by diagonal muscle strand with SOD.

OD3–4, OD3' origin on Pb3 dorsoanteromedially ventral to TEb2, insertion on Eb3 uncinat process dorsoanteriorly and Eb4 uncinat process ventromedial to tip; OD3' splits off ventrally from OD3–4 just posterior to origin and inserts on Eb3 dorsoanteriorly ventral to uncinat process, joins raphe with medial end of Ad3.

OP on posterior surface of Eb4 at and little lateral to uncinat process, ventrally on Cb5 posterolaterally posterior to Ad5, medially partially continuous with SO.

Ad1 weak, on anterodistal bony surface of Eb1 and dorsoanterior end of Cb1 just ventral to Eb1-Cb1 joint.

Ad2 on Eb1 dorsolaterally, joining raphe with lateral end of TEb2, and on anterior surface of Cb2 just ventral to Eb2-Cb2 joint.

Ad3 on dorsoanterolateral surface of Eb3, joining raphe with lateral end of OD3', and on anterior surface of Cb3 just ventral to Eb3-Cb3 joint.

Ad4 dorsally on Eb4 posteriorly ventral to LP, ventrally on Cb4 dorsolaterally medial to Eb4-Cb4 joint.

Ad5 on posterolateral surface of Cb4 (extending onto cartilage tip on one side, but not the other) and dorsolateral surface of Cb5 anterior to OP.

SOD very broad.

RDs adjacent.

Additional remarks. SCL very fine (damage precluded determining whether it is attached to Bb3, posterior end of which is slightly curved ventrally, usually an indication of such attachment). TV4 free from Cb5s. Pb4 and UP4 present. Pb1 and IAC absent. Pb2 toothed.

Notothenioidei

BOVICHTIDAE

Bovichtus veneris (Sauvage), USNM 200412, 107 mm.

Plate 180

Description.

LE1 on raised posterior edge of Eb1 anteriorly, at about mid-length of Eb1. No uncinat process.

LE2 on raised posterior edge of Eb2 anteriorly, at about mid-length of Eb2.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 broadly on Eb4 dorsoposteriorly beginning lateral to uncinat process.

LP on Eb4 joining LE4 insertion posterolaterally.

LI1 mainly on Pb2 dorsoposterior to dorsoanterior process with tendinous attachment ventromedially to anteriormost tip of Pb3.

LI2 on Pb3 dorsally, medial edge of insertion meeting lateral edge of TPb3-Pb4.

TD comprising TEb2 and TPb3-Pb4. TEb2 broad centrally, narrowing laterally and attaching on Eb2 dorsally anterior to LE2 insertion, meeting medial end of Ad2; with mid-longitudinal raphe giving rise to CT sheets covering TD; anterior edge of muscle, between short tendinous raphe on each side of mid-longitudinal raphe, attaching tightly to CT of pharyngeal roof; attaching by filmy CT along mid-longitudinal raphe ventrally between Pb3s to CT to pharyngeal roof; not continuous posteriorly with TPb3-Pb4. TPb3-Pb4 beginning on Pb3 dorsally along medial-edge of LI2 insertion and continuing posteriorly onto medial edge of Pb4 ventral to joint with medial end of Eb4 ventrally, continuous posteriorly by diagonal muscle strap with SOD.

OD3-4, OD3' origin broadly on Pb3 dorsomedially ventral to TEb2, insertion on Eb3 uncinat process anteriorly continuing onto Eb4 uncinat process posteromedially, there joining raphe with OP dorso-laterally; muscle branches (OD3') ventroanteriorly just before insertion on Eb3 uncinat process and inserts on Eb3 dorsally well ventromedial to uncinat process, meeting lateral end of Ad3.

OP dorsally on Eb4 posteriorly beginning on uncinat process (joining raphe with OD3-4) and extending medially to medial end, fibers of medial half passing posteroventrolaterally over those of lateral half and together attaching broadly on Cb5 posterolaterally; ventrodistally tendinously joining tough fascia (not illustrated) covering Ad5 surface; muscle medially not clearly separated from SO.

Ad 1-3 moderately developed. Each beginning on Eb dorsoanterolaterally and extending laterally then ventrally over Cb dorsoanteriorly; Ad2 medial end joining raphe with TEb2; Ad3 medial end just meeting lateral end of OD3'.

Ad4 broadly dorsally on Eb4 ventrally, dorsomedial half overlapped posteriorly by OP, ventrally broadly on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 posteriorly covered by tough fascia, dorsally on Cb4 posterodistally with tendinous connection extending to Eb4 posterodistally (surface of Eb4-Cb4 joint covered by tough fascia (not illustrated), which is continuous with fascia covering Ad5, ventrally on Cb5 mostly anterior to OP.

SOD present.

RDs separated by distance less than half one RD diameter.

Additional remarks. SCL present. TV4 free from Cb5s. Pb1 absent. Pb2 toothed. IAC absent. Pb4 present. UP4 present. Eb4 levator process absent.

PSEDUAPHRITIDAE

Pseudaphritis urvillii (Valenciennes), USNM 344898, 97.2 mm.

Not illustrated

Description.

LE1 on anterior surface of raised bony process on Eb1 mid-dorsoposteriorly (uncinat process absent).

LE2 on anterior surface of raised bony process on Eb2 mid-dorsoposteriorly.

LE3 on tip of Eb3 uncinat process anteriorly.

LE4 on Eb4 dorsoposteriorly lateral to uncinat process.

LP on Eb4 beginning at posterior edge of LE4 insertion and extending well laterally.

LI1 on Pb2 dorsoanteriorly.

LI1' on Pb3 dorsoanterolaterally just ventral to anterolateralmost edge of OD3-4.

Remarks. Presence of LI1 and LI1' very similar to these two muscles in some gobioids.

LI2 on Pb3 dorsoposteriorly medial to medial end of Eb3.

TD comprises TEb2, TPb4a, and TPb4. TEb2 with mid-longitudinal raphe, attached anteroventrally to CT extending anterior to gill arches, raphe giving rise to broad CT sheets covering TD; muscle extending laterally onto Eb2 anterior to LE2 insertion, continuous at posterior end of raphe with TPb4a. TPb4a slender, extending laterally, passing through OD3-4 and attaching ventrally to Pb4 at and lateral to anterolateral attachment of TPb4, continuous posterolaterally by fine, diagonal muscle filament with TPb4. TPb4 relatively broad, on Pb4 medialmost edge at joint with Eb4, questionably with extremely fine tendinous attachment to posteromedialmost edge of Eb3 adjacent to Eb4; continuous posteriorly by fine, crossing diagonal muscle fibers with SOD.

Remarks. This is the only taxon we encountered in which a TD muscle passes through OD3-4. Verification in another specimen is desirable. OD3-4 in some forms (e.g., Odontobutidae) is split by LI2.

OD3-4 origin on Pb3 broadly dorsally ventral to TEb2, anteriorly just medial to LI1' insertion, penetrated by TPb4a just after OD3-4 passes posteriorly from under TEb2, insertion beginning on Eb3 uncinat process anterodorsally and continuing medially to medial edge of Eb4 uncinat process. (See remarks following TD.)

OP dorsally on Eb4 posteroventrally beginning below uncinat process and extending laterally to point below LP insertion, ventrally on Cb5 dorsoposterolaterally, posterior to Ad5 medially.

Ad1-3 absent, but weak GFI on first arch antero-laterally; on arches 2 and 3, GFI begins on Eb dorsoanterior surface and passes to anterior edges of Eb and Cb; GFI best developed on Eb3.

Ad4 dorsally broadly on Eb4 ventrally, beginning anterior to OP laterally and extending laterally to Eb4-Cb4 joint, ventrally on Cb4 broadly.

Ad5 dorsally on Cb4 posterolaterally, ventrally on

Cb5 beginning dorsoposterodistally and extending medially short distance anterior to OP.

SOD present.

RDs separated by space equal to less than half diameter of one RD.

Additional remarks. SCL attached tendinously mid-dorsoposteriorly to posteroventral cartilaginous end of Bb3. TV4 free from Cb5. IAC absent. Pb1 absent. Pb2 toothed. Pb4 and UP4 present. Eb4 levator process absent.

Pseudaphritis is sometimes included in the Bovichtidae, but recent studies (Balushkin, 1992; Eastman and Clarke, 1998) do not support this inclusion.

Dactylopteroidei

Imamura (2000) excluded the Dactylopteridae from the Scorpaeniformes based on several characters and included them with the Malacanthidae in an expanded family Dactylopteridae. He hypothesized the latter action based on eight putative synapomorphies. His first appears to be the most significant, nasals of dactylopterids are fused in both larvae and adults and the nasals of malacanthids [and holocentrids] are fused in larvae, but separate later. He based the malacanthid information on Johnson (1984:491 et seq.). Imamura, thus, equated fusion of the nasal bones with subsequent separation, as found in malacanthids, with fusion of nasal bones without subsequent separation, as found in dactylopterids. We believe that this consideration needs further study; however, for convenience, we maintain Imamura's association of the two families by including them in a single suborder.

Imamura's synapomorphies 2–6, and 8 (absence of supramaxillary, absence of prevomerine teeth, absence of palatine teeth, presence of six branchiostegal rays, absence of toothed plate on Eb2, presence of a TDA circular element) have a wide and varied distribution and we believe should be part of a larger character-based test of interrelationships. He reported that his seventh synapomorphy, adductor mandibulae section 2 subdivided, is "a rare synapomorphy" based on its absence in members of 18 perciform families (he reported 16 families, but we recognize two additional included among his material) and "75 species of Scorpaeniformes . . . listed by Imamura (1996)." We are unable to comment on the seventh synapomorphy, but note there are a great many more families that should be evaluated for it.

DACTYLOPTERIDAE

Dactyloptena macracantha (Bleeker), USNM 224473, 92.7 mm.

Plate 181

Description.

LE1 broadly on Eb1 mid-dorsally.

LE2 on Eb2 mid-dorsally.

LE3 on Eb3 uncinate process anteriorly just ventral to OD3–4 insertion, which is on cartilage tip of process anteriorly.

Remarks. This is the only instance we know of in which LE3 inserts on Eb3 ventral to OD3–4 insertion on Eb3. The condition should be verified in another specimen.

LE4 on Eb4 dorsoposterolaterally.

LP on Eb4 anterolateral to LE4 insertion.

LI1 On Pb3 dorsoanterolaterally.

LI2 on Pb3 dorsoposterolaterally just medial to medial end of Eb3.

TD comprises TPb2, TEb2, and TPb3–Eb3. TPb2 flat, laterally curving, semicircular ribbon of muscle on each side dorsal to TEb2; joined to contralateral TPb2 anteromedially by broad wedge of CT, which narrows to raphe posteriorly; muscle arising from TEb2 anteromedially, becoming fine tendon posteromedially attaching to raphe and contralateral TPb2; attached anterolaterally by CT to dorsoanterior end of Pb2; mid-longitudinal CT areas attached ventrally to CT of pharyngeal roof, giving rise dorsally to filmy CT sheets covering muscles. TEb2 separated from counterpart by same CT areas as TPb2; extending laterally and fanning out more-or-less vertically and attaching to Eb2 anterolaterally lateral to LE2 origin, meeting and attaching partially ventrally to broad Ad2 medially, connected posteroventrally by very fine filaments of muscle to TEb3. TP3–Eb3 finely tendinously on dorsomedial surface of Eb3 and on Pb3 dorsoposterolaterally just posterior to LI2; posteriorly joined by fine crossing strands of muscle with SOD.

OD3–4 origin broadly dorsomedially on Pb3 ventral to TEb2, insertion on Eb3 uncinate process dorsoanteriorly just dorsal to LE3 insertion and on medial edge of Eb4 uncinate process.

OP broadly dorsally on Eb4 ventrally beginning ventral to LE4 insertion and extending medially, broadly ventrally on Cb5 dorsoposteriorly medial to distal end, medially inseparable from SO.

Ad1–3 unusually well developed.

Ad1 extensively on Eb1 beginning on uncinate process laterally and extending laterally, becoming fan-like and attaching to anterior surface of Eb1–Cb1 joint.

Ad2 on Eb2 anterolaterally, overlying lateralmost end of TEb2 and extending laterally to anterior surface of Eb2–Cb2 joint.

Remarks. It is unusual for Ad2 to overlies the lateral end of TEb2.

Ad3 beginning on dorsal surface of Eb3 medial to uncinate process and on Eb3 uncinate process lateral

to LE3 insertion, and extending laterally and fanning out over anterior surface of Eb3-Cb3 joint.

Ad4 dorsally broadly on Eb4 ventrally mostly lateral to OP, ventrally broadly on Cb4 medial to Eb4-Cb4 joint.

Ad5 on posterolateral end of Eb4 and dorsolateral end of Cb5, medially anterior to OP ventrally.

SOD present.

RDs separated by space less than diameter of one RD. Right-side RD incompletely divided longitudinally, joint cross section noticeably larger than that of left side RD.

Remarks. In Imamura's (2000:fig. 9B) illustration of the RDs of *Dactyloptena macracantha*, the diameter of the left-side RD is noticeably larger than that of the right side. Asymmetry of RD size is common in fishes, although usually not differentially so great as in *Dactyloptena*.

Additional remarks. SCL attached mid-dorsally by tendon to posteroventrally extending cartilaginous tip of Bb3. TV4 free from Cb5s. Pb1 cartilaginous. UP4 present, Pb4 absent, but present in *Dactlopterus volitans* (Linnaeus), based on USNM 261386, cleared and. IAC absent. Pb2 toothed. Eb4 levator process absent.

Remarks. Imamura (2000) described some aspects of the dorsal-gill arch musculature of dactylopterids and presented a diagrammatic illustration of the musculature of *D. macracantha*.

Imamura listed several perciform groups, besides dactylopterids, in which TPb2 is circular (he was uncertain the muscle was homologous with TPb2) and indicated that the condition is a percoid [percomorph] apomorphy. The muscle state is much more widely distributed than Imamura recognized; it also occurs, e.g., in Chaunacidae (Paracanthopterygii), Bathymasteridae (Zoarcoidei), and Centrolophidae (Stromateoidei), among several other groups. Because of the various states of TPb2 present in a wide variety of acanthomorphs, the derivation of the circular TPb2, including the loss of its attachment to Pb2, cannot be decided readily.

MALACANTHIDAE

Caulolatilus affinis Gill, USNM 211424, ca. 98 and ca. 100 mm.

Plate 182

Additional material. ② = *Malacanthus brevirostris* Guichenot, USNM 334628, 150 mm.

Description.

LE1 on Eb1 uncinat process at or just lateral to joint with IAC.

LE2 on bony prominence rising from Eb2 mid-dorsoposteriorly and continuing posteriorly onto mid-anterior edge of Eb3; tendon extends length of mus-

cle surface laterally, attaching to bony prominence and continuing posteriorly and attaching to anterior edge of Eb3.

Remarks. Imamura (2000:214) reported that the insertion of LE2 on Eb2 and Eb3 is restricted to malacanthids and nemipterids among the perciforms he examined. We find that in our specimens of *Nemipterus* there is a ligament attaching the posterior edge of Eb2 at the posteroventral margin of the LE2 insertion to the anterior edge of Eb3. We do not equate these two conditions. In malacanthids, LE2 splits its insertion between the closely adjacent margins of Eb2 and Eb3, such that if the bones are forced apart, LE2 splits longitudinally, with one part remaining with Eb2 and the other with Eb3. In nemipterids, the entire muscular insertion of LE2 is on Eb2.

LE3 on Eb3 uncinat process anteriorly.

LE4 on Eb4 beginning on levator process dorsally and extending laterally and meeting LP insertion anteriorly. ② Like *Caulolatilus*, but insertion broadly, ventroanteriorly meeting OD4.

LP on Eb4 at and joining LE4 insertion posteriorly.

LI1 on Pb2 dorsally just posterolateral to joint with IAC.

LI2 on Pb3 dorsolaterally medial to medial end of Eb3, ventromedial edge meeting TPb3-Eb3 laterally.

TD comprises TPb2, TEb2, and TPb3-Eb3. Thick, cup-shaped CT pad arises mid-dorsally from mid-longitudinal raphe extending across TPb2 and TEb2; pad continuous anteriorly with pharyngeal roof CT. TPb2 a bilateral pair of roughly semicircular muscles dorsal to TEb2 medially; each member of pair attaching anteromedially to CT covering dorsoanteriormost end of Pb2 process articulating with IAC and continuous ventrally with CT of pharyngeal roof; posteromedially each member fades into TEb2 and mid-longitudinal raphe. TEb2 attaches to Eb2 along diagonal beginning posteriorly at medial edge of LE2 insertion and extending anterolaterally to point near lateral edge of CT (not illustrated) attaching Eb2 to Eb1 (lateral to LE2 insertion). TPb2-TEb2 not continuous with TPb3-Eb3. TPb3-Eb3 laterally ventral to OD3-4, with mid-longitudinal raphe; muscle in two layers: dorsal and ventral; both layers attach together laterally on Pb3 dorsolaterally at medial edge of LI2 insertion; fibers of dorsal layer with slight change in orientation between portions attaching to Pb3 and Eb3 (change not obvious in smaller specimen); dorsal layer continues posteriorly attaching to posteromedial margin of Eb3; ventral layer extends posteriorly beyond mid-posterior margin of dorsal layer (ventral layer much less discrete in smaller specimen and absent in ②); muscle not continuous posteriorly with SOD (SOD absent, probably anomalously, in smaller specimen). ② TPb2-TEb2 continuous posteriorly with SOD; TPb3-Eb3 muscle strap

attaching dorsally to Eb3 along posteromedial edge (as in *Caulolatilus*), but ventrally attaching to Pb3 dorsoposteriorly posterior to Pb3-Eb3 joint.

CPb fine muscle thread, easily overlooked, separated by thin epithelial tissue from Pbs, extending posteriorly from Pb2 anterolaterally to UP4 laterally, with short, fine branch extending medially anterior to Pb3 and another medially anterior to UP4; medial branches absent in smaller specimen. ② Slightly better developed, but beginning as continuation from anteriorly extending SO longitudinal fibers medial to Pbs, extending anterolaterally between Pb2 and Pb3 (no extension anterior to Pb2), then posteriorly along lateral surfaces of Pb3 and UP4, with medial branch extending anterior to UP4.

Remarks. Of those taxa possessing CPb (Table 9), it is most poorly developed in malacanthids, and probably vestigial; considerable variation in its manifestation is probably to be expected.

OD3, OD4 originate as slender CT pad attaching along Pb3 dorsomedial edge; posterior half of origin is ventroposterior to TPb2 and TEb2 in larger specimen, but completely ventral to TPb2 and TEb2 in smaller specimen. Muscle divides into OD3 and OD4 well before inserting on Eb3 dorsoanteriorly just ventral to tip of uncinat process and on Eb4 dorsoposteriorly, beginning about midway between medial end and levator process and extending laterally to medial edge of cartilage tip of levator process; tiny cartilaginous tip of Eb4 uncinat process sandwiched between, partially overlain by, and obscured from view by OD3 and OD4 muscle insertions. ② OD3 and OD4 separate almost immediately posterior to insertion; OD4 passes dorsal to all bony Eb4 uncinat process; OD3' present (anomalously?) on one side, separates ventrally from joint origin of OD3 and OD4 and inserts on Eb3 dorsally well ventral to lateral end of OD3.

OP dorsally on Eb4 posteriorly beginning near medial end and extending laterally to below levator process, overlapping medial fibers of Ad4 posteriorly; ventrally, broadly on Cb5 beginning well medially along PCI attachment and extending laterally to just medial to distal end.

Ad1–3 absent, but GFM1s 1–3 (not illustrated) well developed; on anterior margins of Eb1 and Cb1, but beginning on dorsoposterolateral surfaces of Eb2 and Eb3 and attenuating distally and attaching along anterior surface of respective Cb.

Ad4 dorsally on Eb4 posteroventrally, beginning medially below levator process and anterior to dorsolateralmost OP fibers and extending laterally almost to distal end; ventrally on Cb4 dorsoposteriorly beginning medially a short distance from lateral end and joining Ad5 attachment and extending laterally to Eb4-Cb4 joint medially.

Ad5 beginning dorsally on posteriorly extending

cartilaginous process at distal end of Cb4 and continuing a short distance on Cb4 medially, meeting Ad4 ventrally; ventrally on Cb5 dorsodistally extending a short distance medially anterior to lateralmost OP fibers.

SOD present, well posterior to TPb3-Eb3, moderately wide (absent, probably anomalously, in smaller specimen). ② SOD broad, joined mid-anteriorly to TPb3-Eb3.

RDs adjacent; separated by distance half diameter of one RD in smaller specimen and ②.

Additional remarks. SCL attached mid-dorsally to elongate ventroposteriorly extending cartilaginous posterior end of Bb3 (only ObV3 attaches to it). TV4 free from Cb5s. Pb2 toothed. Pb4 and UP4 present.

Callionymoidei

DRACONETTIDAE

Draconetta oregona Briggs and Berry, USNM 159234, 110 mm.

Plate 183

Description.

LE1 on raised mid-dorsoposterior bony edge of Eb1 (no uncinat process).

LE2 on mid-dorsoposterior bony edge of Eb2.

LE3 tendinously on dorsal edge of Eb3 lateral to uncinat process.

LE4 massive, dorsally on expanded posterior surface of Eb4 well lateral to joint with Eb3 uncinat process.

LP on dorsal surface of Eb4 between lateral edge of LE4 insertion and distal end of Eb4.

LI1 on dorsoanteriormost surface of Pb3, which overlies all of dorsal surface of Pb2 except for anteriormost cartilaginous end.

LI2 on Pb3 posterolaterally medial to medial end of Eb3.

TD broad, continuous, comprising TEb2, TEb3, and, very doubtfully, TPb2. Questionable TPb2 a thin, slender posterolaterally convex strip of muscle bordering TEb2 anteriorly, widening laterally as it extends dorsal to TEb2 and inserts on Eb2 among TEb2 fibers as they pass laterally onto Eb2; not attached to Pb2, see remarks). TEb2 with mid-longitudinal raphe continuing posteriorly on all but posterior section of TEb3; raphe giving rise to filmy CT covering TD; TEb2 attaching mid-anteriorly to CT of pharyngeal roof and amid sparse, anteriorly extending longitudinal muscle fibers, attaching anteroventrolaterally to dorsoanterior ends of Pb2 and Pb3 (unusual for TEb2 to attach to Pb2); as muscle extends laterally, anterior fibers twist posteroventrally over posterior fibers and extend onto Eb2 dorsally to attach anterior to LE2 insertion, joining raphe with medial end of Ad2; posterior fibers attach to posterior

edge of Eb2 medial to LE2 insertion; continuous posteriorly with TEb3. TEb3 on Eb3 dorsoposteromedially ventral to OD3–4 insertion, continuous posteriorly by fine muscle filament with SOD.

Remarks. Most probably the questionable TPb2 is part of TEb2 and is treated as such for cladistic purposes. Attention is drawn to it here because TPb2 is present in the Callionymidae, which is the sister group to Draconettidae.

CPb comprising subcutaneous filaments of muscle difficult to free from skin, simple strip passing around Pb2 on each side and continuing down lateral and medial margins of Pb3, then meshing with matrix of subcutaneous muscle extending posteriorly from Pb3 and becoming SO.

Remarks. The presence of CPb is evidence for close relationship with Callionymidae, which has a far more complex development of dorsal gill-arch musculature that obscures the long-accepted sister-group relationship between the Callionymidae and Draconettidae.

OD3–4 origin on Pb3 dorsomedially ventral to TEb2, insertion on anterior surface of Eb3 uncinat process and posterior surface of Eb4 where Eb4 articulates with Eb3 uncinat process.

OP on most of posterior surface of Eb4, fused indistinguishably ventrolaterally with Ad5, broadly on Cb5 dorsally continuous with Ad5, distinguishable medially from SO mainly by abrupt change from thickness of OP to very thin SO.

Ad1 attaching on anterior surface of Eb1 just anteromedial to medial edge of LE1 and extending laterally, fanning out distally, and attaching across anterior surfaces of distal ends of Eb1 and Cb1.

Ad2 with anterior and posterior sections, anterior section on Eb2 dorsally meeting lateral end of TEb2, posterior section dorsally meeting anterior edge of LE2 insertion, sections fuse laterally, fan out and attach across anterior surfaces of distal ends of Eb2 and Cb2.

Ad3 with anterior and posterior sections, anterior section on Eb3 dorsally, posterior section dorsally meeting anterior edge of LE3 insertion, sections fuse laterally, fan out and attach across anterior surfaces of distal ends of Eb3 and Cb3.

Ad4 (obscured in posterior view) dorsally broadly on Eb4 ventral surface anterior to OP, ventrally broadly on Cb4 dorsal surface medial to Eb4-Cb4 joint.

Ad5 completely fused medially with OP (including attachment to Cb5), attaching anteriorly to posterodistal surfaces of Eb4 and Cb4.

SOD very slender.

RDs adjacent.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Tiny cartilaginous Pb1 attached to medial

tip of Eb2. Pb4 and UP4 absent. Eb4 cartilage-tipped uncinat and levator processes absent.

CALLIONYMIDAE

Callionymus lyra Linnaeus, USNM 197584, 3 specimens, 86.3–128 mm.

Plates 184.1, 184.2

Additional material. ② = *Callionymus filamentosus* Valenciennes, USNM 232253, 68.7 mm.

Description.

Remarks. Kayser (1962) described and illustrated the gill-arch musculature and skeleton of *C. lyra*. Although we generally agree with his findings, his description is brief and does not do justice to the extreme complexity exhibited by these muscles in *Callionymus*. Additionally we report a muscle (CPb) he did not include. Winterbottom (1974b:fig. 23) provided a redrawn version of one of Kayser's figures.

LE1 on Eb1 dorsodistally, joining tough CT raphe ventromedially with distal end of M. Pb3-Eb1.

LE2 on dorsodistal end of Eb2 meeting RecD3 dorsoposteromedially and M. Pb3-Eb4-Eb2-Cb3 distally.

LE3 absent (see LE4).

LE4 massive, inserts on CT binding distal ends of Eb3 and Eb4 and is joined there by posterior end of RecD4 and anterior end of Ad5; posteroventrally joins LP anteroventrally (see LP for variation in ②).

Remarks. Either LE3 and LE4 are fused or LE3 has been completely lost; we arbitrarily opt for the latter interpretation because the general configuration exhibited by LP and the questionable muscle is like that of LP and LE4 of many fishes; Kayser (1962) assumed that LE3 and LE4 are fused.

LP joins LE4 insertion posteriorly on Eb4 and joins Ad5 dorsally. ② LP and LE4 joined tendinously and only lateralmost edge of LE4 portion attached to Eb4 near distal end; muscles together forming "sling" (Stiassny and Jensen, 1987:284), with tendon from LP extending ventrally and attaching to Cb5 anterior to OP; Ad5 absent.

LI1 on Pb3 broadly dorsoanterolaterally at and dorsal to M. Pb3-Eb1 origin.

LI2 on Pb3 dorsoposteriorly medial to M. Pb3-Eb4-Eb2-Cb3 origin on Pb3.

TD comprises TEb2, TPb2, and TEb4. TEb2 thin, bilateral muscle pair, continuous membranously dorsal to Pb3s and from mid-longitudinal pharyngeal roof muscle fibers, attaching sheet-like along posterolateral surface of Eb2. TPb2 a bilateral pair of semicircular ribbons attaching to CT surrounding anterior edges of Pb3 and Pb2 (Pb2 almost entirely ventral to Pb3), fusing posteromedially with TEb2 and TEb4. TEb4 comprising anterior and posterior por-

tions; anterior portion with mid-longitudinal raphe, posterior portion uninterrupted, both portions fusing together laterally and inserting on Eb4 dorsomedially ventral to OD4; joined by CT mid-ventrally to SOD mid-dorsally when SOD is present.

CPb originates as SO longitudinal fibers extending anteriorly dorsal to pharyngeal roof tissue, dividing well posterior to gill arches with branch on each side extending around Pb2 and Pb3 and attaching antero-laterally to Eb2 and Pb2 ventrally, where the two bones meet, and to Pb3 posterolaterally.

OD3 absent.

OD4 origin on Pb3 dorsally ventral to TEb2, insertion on bony Eb4 uncinat process dorsoanteriorly.

M. Eb1-Cb1 attaches dorsomedial end of Eb1 to dorsoanterodistal end of Cb1; muscle joins CT surrounding distal end of Cb1, which is also joined by anterior end of RecD2.

Remarks. The skeletal elements to which M. Eb1-Cb1 attaches are the same as those that define Ad1 in other acanthomorphs, but the position of the Ad1 attachment on Eb1 is closer to the distal end of the bone and spans the Eb1-Cb1 joint, very unlike M. Eb1-Cb1.

M. Pb3-Eb1 origin on Pb3 anterolaterally at and ventral to lateral edge of LI1 insertion, insertion on posterodistal edge of Eb1, there joining raphe with LE1 insertion and raphe of RecD2 with RecD3.

M. Pb3-Eb4-Eb2-Cb3 origin beginning on Pb3 dorsoposterolaterally and continuing onto Eb4 dorsomedially along attachment of TEb4, insertion along posterior edge of LE2 insertion on Eb2 and with raphe joining RecD3 and RecD4 to dorsodistal end of Cb3.

OP dorsally on posterior surface of bony Eb4 uncinat process, ventrally on Cb5 posterolateral surface, joining small raphe with Ad5 ventrolaterally at dorsodistal end of Cb5.

Ad1–3 absent.

Ad4 dorsally on Eb4 posterolaterally (mostly overlapped posteriorly by OP and Ad5), ventrally on Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 posteriorly on Cb5 dorsodistally, dorsoanterolaterally attaching joining distal ends of Eb4 and Eb3 and to which LE4 inserts, dorsoanteriorly joining raphe with LP insertion, ventroanteriorly fusing indistinguishably with RecD5 (see also Remarks prefacing RecD2). ② Ad5 absent.

Remarks. Kayser (1962:413; fig. 35) treated the muscle we identify as Ad5 as a fusion of two muscles “Musculus pharyngo-arcualis I + II.” He illustrated the muscle as being divided by a raphe into right and left halves. Based on his illustration of *Ammodytes* in the same paper (1962:fig. 15), he considered the fused muscle to comprise the muscles we designate as Ad5 and OP. Although we agree that Ad5 is involved in a fusion, we find that the composition is

Ad5 + RecD5, and the direction of the fusion is anterior-posterior. OP is distinct. We were only able to resolve the composition of the fusion in *C. lyra* because Ad5 is completely absent in *C. filamentosus*, but RecD5 is distinct and very similar to RecD2–4.

RecDs. The next four muscles are designated as *recti dorsales*, a name coined by Winterbottom (1974b:259) to apply to muscles that interconnect epibranchials of successive arches. He included similar muscles in *Callionymus lyra*, although the connections do not agree entirely with his definition, are more complex, and are possibly synapomorphic for the family. In the two larger specimens in USNM 197584, the RecDs appear to be individual muscles. In the smallest specimen RecD3 and 4 each appears to comprise two muscles (Plate 184.2D), a RecD and an underlying muscle, RecCb, attaching the distal ends of successive Cbs. In all three specimens RecD5 is fused posteriorly with Ad5 and appears to include a fused RecCb anteroventrally. In the specimen of *C. filamentosus*, we only confidently observed RecCbs between arches 2 and 3 and 3 and 4. The RecDs of *Callionymus* do not appear to be homologous with those of the only other acanthomorph, *Mene*, in which they are present.

RecD2 anteriorly on distal end of Cb1, there joining raphe with M. Eb1-Cb1, posteriorly joining raphe with and anterior end of RecD3 on distal ends of Eb1 and Cb2.

RecD3 anteriorly joining raphe with posterior end of RecD2 on Eb1 and Cb2 and posteriorly joining raphe with anterior end of RecD4 on distal ends of Eb2 and Cb3.

RecD4 anteriorly joining raphe with posterior end of RecD3 on distal ends of Eb2 and Cb3, and posteriorly joining raphe with anterior end of RecD5 on distal ends of Eb3, Eb4, and Cb4.

RecD5 anteriorly on distal ends of Eb3, Eb4, and Cb4, posteriorly fusing with Ad5 on Cb5 anterodistally. ② Posteriorly on anterodistal end of Cb5; Ad5 absent.

SOD present in only one of three specimens (113 mm SL); very thin, slender, completely ventral to TEb4, with median raphe attaching to ventral surface of TEb4. ② Absent.

RDs separated by distance less than half diameter of one RD.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Pb4 and UP4 absent. Pb2 toothed. IAC absent. Cartilage tipped Eb4 uncinat and levator processes absent.

Kayser (1962:412) designated the muscles we call M. Eb1-Cb1, M. Pb3-Eb1, and M. Pb3-Eb4-Eb2-Cb3 as *M. obliquus inferior* 1–3. Despite their different attachments, Kayser considered them to be serial homologs and different from OD4, which he also recognized in *C. lyra*. Kayser did not report the presence

of OD3 in *C. lyra*, and we note that it is absent. Winterbottom (1974b:253–254) considered a variety of bilaterally paired transverse muscles joining Pbs to Ebs as ODs. He included Kayser's *obliqui inferiores* among them. The muscle in *Callionymus* that would be interpreted as OD3 does not include Eb3 among its attachments and we do not consider it to be homologous with OD3 in other actinopterygians. The presence and attachments of OD3 and OD4 in actinopterygians are so consistent that we reserve the terms OD3 and OD4 for them.

Usually, PCI is attached to Cb5 muscously or by short tendon, but in *Callionymus* and *Trachelochismus* (Gobiesocidae) it is attached by a long, slender tendon. These two families, together with the Dracottidae, were hypothesized by Gosline (1970) to form a natural group.

GOBIESOCIDAE

Trachelochismus sp., USNM 339196, 57.1 mm.

Plate 185

Description.

LE1 on Eb1 dorsally at about mid-length; uncinat process absent.

LE2 on Eb2 posteriorly near distal end.

LE3 absent.

LE4 on Eb4 dorsodistally.

LP on Eb4 at and posterior to LE4 insertion.

LI1 on Pb3 dorsoanteriorly.

LI2 on Pb3 dorsally lateral to TPb3-Eb4 attachment.

TD comprises TEb1, TEb2, and TPb3-Eb4. TEb1 a slender filament on medial tip of Eb1, continuous posteriorly with TEb2. TEb2 broad, flat mid-dorsally, with median longitudinal raphe, muscle narrowing laterally, attaching to Eb2 dorsomedially, and posteriorly continuous with Eb4 portion of TPb3-Eb4. TPb3-Eb4 delaminating (bilaterally) from posteroventral surface of TEb2, extending laterally, and having two separate attachments to Pb3, one curving anteriorly, passing ventral to OD3–4 origin, and attaching to dorsal surface of Pb3, the other extending laterally and attaching to Pb3 near medial ends of Eb3 and Eb4; Eb4 portion slender, on medial end of Eb4, continuous posteriorly with SOD.

Remarks. Although undoubtedly homoplastic, TEb1 is known otherwise only in certain labrid taxa.

OD3–4 originates on Pb3 and, unusually, on medial end of Eb2 anteriorly ventral to TEb2, overlying lateral attachments of TPb3-Eb4 to Pb3, and inserts on dorsoanterior surface of proximal half of Eb3 and posterior edge of proximal quarter of Eb4.

OP, if present, inseparable from SO.

Ad1 on mid-anterior surface of Eb1 and dorsoanterior surface of Cb1 just ventral to Eb1-Cb1 joint.

Ad2 on much of distal half of Eb2 anterior surface,

extending anterolaterally and attaching to posterodistalmost end of Eb1 (unusual), anterior surface of Cb2 just ventral to Eb2-Cb2 joint, and dorsolateral edge of CT joining Eb1 and Eb2.

Ad3 on most of medial half of Eb3 anterior surface, extending anterolaterally and attaching to posterodistalmost edge of Eb2 (unusual), at and just ventral to Eb3-Cb3 joint, and dorsolateral edge of CT joining Eb3 and Cb3.

Ad4 dorsally on Eb4 posteriorly beginning at about mid-length of Eb4 and extending laterally almost to end of bone, ventrally on Eb4 for about distance equal to dorsal attachment.

Ad5 on anterolateral surface of Cb5, extending onto posterodistal half of surface of Cb4 and continuing onto posterodistal end of Eb4.

SOD present, continuous anteriorly with TPb3-Eb4.

RDs separated by space greater than twice diameter of one RD.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1, Pb2, Pb4, and UP4 absent. Eb1, Eb3, and Eb4 uncinat processes absent. Eb4 levator process absent. Medial end of Eb3 much larger than that of Eb4. PCI attaches by long slender tendon to distal end of Cb5.

Blennioidei

Remarks. Springer (1993) defined the Suborder Blennioidei and its included six families: Blenniidae, Chaenopsidae, Clinidae, Dactyloscopidae, Labrisomidae (monophyly not hypothesized), and Tripterygiidae. He was unable to resolve the intra-relationships of the families, but hypothesized that the Tripterygiidae are the sister group of the other five families. Hastings and Springer (1994) hypothesized the intra-relationships of the Chaenopsidae, placing *Neoclinus* as sister group of the other genera.

Although all of the gill-arch specializations that characterize blennioids are found among other acanthomorph taxa, the number and combination of these specializations are distinctive. Specializations include: TPb2 absent (except a vestige in Labrisomidae); Pb3 muscously naked dorsoanteriorly; attachment of TV4 to Cb5; absence of cartilage tipped Eb1, Eb3, and Eb4 uncinat processes and Eb4 levator process; PCI broadly on Cb5, extending to distal end and joining raphe with OP ventrally (in all families except Dactyloscopidae, in which the two muscles just fail to meet). All blennioids lack IAC, Pb2, Pb4, and UP4. LI1 attaches to Pb3, which is also a specialized state; however, Pb2 is absent.

The most restricted of these specializations are the muscously naked dorsoanterior surface of Pb3 and the combination of the attachment of PCI to include the distal end of Cb5 and the muscle's joining a raphe

with OP ventrally (we consider failure of PCI to join a raphe with OP in the Dactyloscopidae to be derivative for blennioids). The combined PCI-OP state occurs in centrogeniids, sciaenids, nemipterids, pinguipedids, mastacembelids, lethrinids (*Monotaxis* and *Gymnocranius*, but PCI just failing to reach distal end of Cb5 in *Lethrinus*, see description, additional remarks).

TRIPTERYGIIDAE

Ruanoho decemdigitatus (Clarke), USNM 92.0 mm;
USNM 339242, 73.6 mm.

Plate 186

Description.

LE1 broadly on expanded bony dorsoposterior edge of Eb1 (no uncinat process).

LE2 broadly on expanded bony dorsoposterior edge of Eb2.

LE3 anteriorly on dorsoposterior edge of Eb3 all bony uncinat process, joining raphe with dorsolateral edge of OD3–4 on Eb3.

LE4 large, on Eb4 dorsolaterally, extending to distal end of bone.

LP on Eb4 posterior to LE4 insertion.

LI1 on Pb3 beginning on anterolateralmost edge and continuing posteriorly onto dorsoanterior surface ventral to TEb2 (Pb2 absent).

LI2 on Pb3 dorsoposterolaterally medial to medial end of Eb3, aligned along lateral edge of TPb3.

TD comprises TEb2 and TPb3. TEb2 a broad band interrupted by mid-longitudinal raphe, which gives rise dorsally to filmy CT and is attached ventrally to CT of pharyngeal roof; attaches on Eb2 dorsally well medial to LE2, continuous posteriorly by diagonal strand of muscle with TPb3. TPb3 on bony surface of Pb3 dorsolaterally along medial edge of LI2 insertion, extending posteriorly opposite to medial end of Eb4.

OD3–4 origin on Pb3 dorsally ventral to TEb2, insertion on Eb3 dorsoanterior surface medial to LE3 (joining ventromedial edge of LE3) and on mid-dorsal surface of Eb4.

OP broadly dorsally on Eb4 coincident with ventroposterior edge of LP insertion; broadly ventrally on Cb5 almost coincident with PCI attachment; medially incompletely separable from SO.

Ad1 on Eb1 bony surface anterodistally and Cb1 anteriorly just medial to distal end of bony surface.

Ad2 broadly on most of Eb2 bony surface dorsoanteriorly lateral to TEb2, narrowly on anterodistalmost bony surface of Cb2.

Ad3 broadly on Eb3 bony surface dorsoanteriorly ventral to OD3–4, narrowly on Cb3 anterodistalmost bony surface.

Ad4 broadly on Eb4 dorsolaterally anterior to OP,

extending very broadly onto Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 on Cb4 posterolaterally (extending medially anterior to OP) and on Cb5 anterior to OP attachment, beginning at distal end and extending medially, joining raphe with PCI.

SOD absent.

RDs well separated in larger specimen, much less so in smaller specimen.

Additional remarks. SCL free from Bb3. TV4 ventrally free across Cb5s, but with divided dorsal attachment to lateral surface of anterior end of each Cb5. IAC, Pb1, Pb2, Pb4, and UP4 absent. Cartilage tipped uncinat process on Eb1, Eb3, and Eb4 absent. Eb4 levator process absent.

Lepidoblennius marmoratus (Macleay), USNM 201625, 82.1 mm; USNM 201626, 90.7 mm.

Plate 187

Description.

LE1 broadly on expanded bony dorsoposterior edge of Eb1.

LE2 broadly on expanded bony dorsoposterior edge of Eb2.

LE3 anteriorly on dorsoposterior edge of Eb3 all bony uncinat process.

LE4 massive, on entire dorsolateral surface of Eb4 beginning medially at posterolateral edge of OD3–4.

LP massive, fused with LE4 posteroventrally, extending posteroventrally ventral to Eb4 and joining raphe with dorsal end of Ad5; tendon from raphe extends to Cb5; muscle fuses with OP medially; some posteromedial fibers continuous ventrally with OP.

LI1 on dorsoanterolateralmost edge of Pb3 (Pb2 absent).

LI2 on Pb3 dorsoposterolaterally, paralleling medial ends of Eb3 and Eb4.

TD comprises TEb2 and TPb3. TEb2 broadly interrupted medially, becoming thin, fascia-like and attaching to broad, flat Pb3 dorsal surfaces; fascia also continuous with TPb3 anteriorly; attaching laterally on Eb2 dorsally well medial to LE2, continuous posteriorly by diagonal muscle strand with TPb3. TPb3 on Pb3 dorsolaterally at medial edge of LI2 insertion, ending posteriorly medial to medial end of Eb4.

OD3–4 origin on Pb3 dorsally ventral to TEb2, insertion on Eb3 dorsoanterior surface medial to LE3 insertion (joining ventromedial edge of LE3) and on mid-dorsal surface of Eb4.

OP dorsally, broadly on Eb4 coincident with ventroposterior edge of LP insertion; ventrally broadly on Cb5 joining raphe ventrolaterally with PCI attachment to Cb5, medially incompletely separated from SO.

Ad1 on Eb1 bony surface anterodistally and Cb1 bony surface medial to distal end.

Ad2 broadly on most of Eb2 bony surface dorsoanteriorly lateral to TEb2, narrowly on dorsoanteriormost bony surface of Cb2.

Ad3 broadly on most of Eb3 bony surface dorsoanteriorly, narrowly on Cb3 bony anterodistalmost surface.

Ad4 broadly on Eb4 dorsolaterally anterior to OP, very broadly on Cb4 medial to Eb4-Cb4 joint. (Not visible in illustration.)

Ad5 on Cb4 posterolaterally (extending medially anterior to OP), on Cb5 anterolaterally anterior to OP, some fibers continuous with OP.

SOD absent, but on one side of only one specimen, a slender filament of SO muscle extends dorsomedially, passes dorsal to the RD on that side and returns to SO between the two RDs.

RDs separated by space less than half diameter of one RD.

Additional remarks. SCL present. TV4 dorsal fibers attach to lateral surface of anterior end of Cb5 on each side, ventral fibers continuous across Cb5s. IAC, Pb1, Pb2, Pb4, and UP4 absent. Cartilage tipped uncinat process on Eb1, Eb3, and Eb4 absent. Eb4 levator process absent.

BLENNIIDAE

Parablennius gattorugine (Linnaeus), USNM 276284, 94.4 mm.

Plate 188

Additional material. ② *Parablennius tasmanianus* (Richardson), USNM 276284, 81.3 mm; ③ *Scartella cristata* (Linnaeus), USNM 208445, 105 mm; ④ *Scartichthys gigas* (Steindachner), USNM 227556, 77.8 mm; ⑤ *Istiblennius edentulus* (Schneider and Forster), USNM 334144, 108 mm.

Description.

Remarks. Although the disposition of the muscles in all the taxa is generally similar, information on ② ③ ④ ⑤ should be considered limited to the specific features described.

LE1 on tip of all bony Eb1 uncinat process and tendon attaching posterior end of insertion to Eb2. ② Like *P. gattorugine*. ③ ④ ⑤ Restricted to bony process and surface of Eb1.

LE2 enveloping pointed, vertical bony mid-dorsal Eb2 process and on tendon attaching posterior end of insertion to Eb3. ② Like *P. gattorugine*. ③ ④ ⑤ Restricted to bony process and surface of Eb2.

LE3 on raised edge of bony Eb3 uncinat process and on CT tendon attaching Eb3 to Eb4. ② Like *P. gattorugine*. ③ ④ ⑤ Restricted to bony process and surface of Eb3.

LE4 on Eb4 dorsally near lateral end of bony sur-

face, joining raphe ventroanteriorly with OD4. ② Does not join raphe.

LP joining raphe with lateral edge of LE4 insertion and extending laterally to end of bony portion of Eb4.

LI1 on lateral surface of dorsal Pb3 articulating process near joint with Eb2. ② ③ ④ ⑤ Like *P. gattorugine*.

LI2 on Pb3 dorsolaterally medial to medial end of Eb3. ② ③ ④ ⑤ Like *P. gattorugine*.

TD comprises TEb2 and TPb3. TEb2 muscle changes to CT medially as muscle passes dorsal to essentially naked Pb3 dorsal facets, attaches on Eb2 anterior surface ventral to pointed mid-dorsal bony process, there joining raphe with dorsal edge of Ad2; continuous by fine strand of muscle posteriorly with TPb3. TPb3 on Pb3 dorsally medial to LI2 insertion and medial end of Eb4, abutting but not continuous posteriorly with SOD. ② Comprises TEb2 and TPb3; anomalous strap of TEb2 attaches to Eb4 dorsomedially on one side. ③ Comprises TEb2 and TPb3-Eb4; TEb2 uninterrupted; TPb3-Eb4 attaches to Pb3 dorsolaterally ventral to attachment on Eb4 medially. ④ Comprises TEb2 and TPb3-Eb4; TEb2 broadly continuous across Pb3s, notched anteriorly, with median longitudinal raphe; TPb3-Eb4 attached to Pb3 anterior to medial end of Eb4 and to Eb4 dorsomedially. ⑤ TD like *P. gattorugine*, but TEb2 is continuous posteriorly across Pb3s and attaches on dorso-posterior surface of Eb2.

OD3-4 origin on lateral edge of Pb3 articulating facet, insertion very finely on dorsal edge of bony Eb3 uncinat process, joining raphe there with LE3 insertion, and massively on Eb4 dorsally joining raphe there with ventromedial edge of LE4 insertion. ② ③ ⑤ Like *P. gattorugine*. ④ Insertion only on Eb4 (OD4).

Remarks. When present in any of the taxa, the insertion on Eb3 consists at most of a fine muscle strand. We think it probable that the presence or absence of the attachment may vary within a taxon.

OP dorsally broadly on Eb4 posteriorly, overlapping Ad4 posteromedially; ventrally on Cb5 posterodistally, joining raphe ventrolaterally with PCI. ② ③ ④ ⑤ Like *P. gattorugine*.

M. Eb4-F, dorsally thin, sheet-like, on anterodistal bony edge of Eb4 ventrally anterior to Ad4, extending ventromedially, becoming more string-like and meshing into SO. Also present, at least, in ② ③ ⑤.

Ad1 dorsally on anterolateral half of bony surface of Eb1, ventrally on lateral third of bony surface of Cb1. ② ③ ④ ⑤ Present in all taxa.

Ad2 dorsally on anterolateral bony surface of Eb2 joining raphe with distal end of TEb2 ventrally, ventrally on anterodistal bony surface of Cb2. ② ③ ④ Present in all taxa. ⑤ Extending from dorsomedialmost bony surface of Eb2 to anterodistal bony surface of Cb2, joining raphe posteriorly with TEb2.

Ad3 dorsally on anterolateral half of Eb3 bony surface, ventrally on dorsodistal bony surface of Cb3. ② ③ ④ ⑤ Present in all taxa.

Ad4 dorsally on ventral surface of lateral half of Eb4 anterior to OD and posterior to M. Eb4-F, ventrally on Cb4 dorsally medial to Eb4-Cb4 joint and anterior to Ad5. ② ③ ④ ⑤ Present in all taxa.

Ad5 dorsally on Cb4 posterolaterally, ventrally on dorsolateral half of Cb5. ② ③ ④ ⑤ Present in all taxa.

SOD present. ② ④ ⑤ Present; questionably absent in ③ (needs verification in another specimen).

RDs adjacent. ② ③ ④ ⑤ Like *P. gattorugine*.

Additional remarks. SCL present. TV4 in two sections: broad, uninterrupted ventroanterior section and narrow, interrupted slightly dorsoposterior section attaching to anterolateral surface of Cb5. ② ③ ④ ⑤ Like *P. gattorugine*. IAC, Pb1, Pb2, Pb4, and UP4 absent in all taxa. Eb1, Eb3, and Eb4 cartilage-tipped uncinat processes absent.

DACTYLOSCOPIDAE

Dactylagnus mundus Gill, USNM 205741, 109 mm; USNM 205742, 2 specimens, 92.2–92.7 mm.

Plate 189

Description.

LE1 broadly on Eb1 mid-dorsally.

LE2 broad based, beginning on dorsoposteromedial edge of Eb2 and continuing laterally onto CT joining Eb2 and Eb3, about half insertion on Eb2, half on CT.

LE3 absent.

LE4 broadly on most of bony anterior edge of Eb4 lateral to OD3–4.

LP on Eb4 at and paralleling entire posterior edge of LE4 insertion.

LI1 broadly on ventral surface of anterior arm of Pb3 (Pb2 absent).

LI2 on Pb3 dorsolaterally medial to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 broad with mid-longitudinal raphe attaching mid-ventrally to CT of pharyngeal roof and giving rise to filmy CT sheets attaching to skull; muscle not overlying dorsal articulating surfaces of anterior Pb3 arms, extending dorsolaterally to point on Eb2 ranging from opposite medial edge of LE2 insertion to mid-point of insertion (less extensive than any other blennioids except tripterygiids); posteriorly dorsal to, and not continuous with, TPb3-Eb4. TPb3-Eb4 narrowly on Pb3 dorsoposterolaterally, continuing posteriorly and attaching to much of posterior edge of Eb4, posteriorly dorsal to, and not continuous with, SOD.

OD3–4 origin on Pb3 dorsolaterally ventral to TEb2, insertion on Eb3 dorsally in area near and dorsal to all bony uncinat process and on most of Eb4

medial and dorsal to all bony uncinat process, paralleling TPb3-Eb4 attachment to Eb4.

OP dorsally on Eb4 beginning a little medial to distal end and extending medially about half length of bone, medially indistinguishable from SO, ventrally broadly on Cb5 beginning near distal end and extending medially joining raphe ventrally with attachment of PCI on Cb5 distally, laterally overlapping much of slender Ad5.

Ad1–3 absent.

Ad4 hidden in posterior view, distinguishable ventrally by broad, separate insertion on Cb4 anterior to attachment of Ad5, dorsally on Eb4 ventrally, apparently fusing with OP posteriorly.

Ad5 slender, on dorsoposterior surfaces of distal ends of Cb4 and Cb5, medial edge posteriorly overlapped by OP laterally.

SOD present.

RDs separated by space less than diameter of one RD.

Additional remarks. SCL free from Bb3. TV4 interrupted, attaching to lateral surface of each Cb5, few, if any, muscle strands continuous across Cb5s ventrally. IAC, Pb1, Pb2, Pb4, and UP4 absent. Eb4 levator process absent.

CLINIDAE (MYXODINAE)

Gibbonsia evides (Jordan and Gilbert), USNM 152005, 2 specimens, 116–126 mm.

Plate 190

Additional material. ② = *Heterostichus rostratus*, USNM 132367, 208 mm.

Remarks. *Gibbonsia* and *Heterostichus* are members of the oviparous, putatively least specialized clinid tribe Myxodini.

Description.

LE1 broadly on dorsoposterior bony expansion of Eb1.

LE2 broadly, anteriorly on dorsoposterior bony expansion of Eb2.

LE3 on Eb3 dorsoanteriorly lateral to tip of all bony uncinat process.

LE4 broadly on dorsodistal bony surface of Eb4. ② Joins raphe ventrally with OP lateral section dorsally.

LP at and posterior to LE4 insertion.

LI1 on lateral edge and much of ventral surface of Pb3 anterior process.

LI2 on Pb3 dorsoposterolaterally at medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 sinuoidal, with mid-longitudinal raphe anteriorly, which gives rise to filmy CT covering muscles dorsally; attaching anteriorly by tough fascia to Pb3s and pharyngeal roof (most of dorsal surface of Pb3 anterior

processes not covered by muscle); attaching over most of Eb2 dorsal surface, meeting anterior edge of LE2 insertion; overlapping, but not continuous with, TPb3-Eb4 mid-anteriorly. TPb3-Eb4 broadly dorsally beginning anterior to LI2 insertion, continuing medial to insertion and onto dorsomedial Eb4 surface, not continuous with SOD.

OD3–4 origin broadly on lateral edge of Pb3 posterolaterally ventral to TEb2, insertion on medial edges of all bony Eb3 and Eb4 uncinat processes. ② Insertion continues dorsoposteriorly across Eb4 and joins raphe with OP medial section dorsally.

OP dorsally beginning on Eb4 uncinat process posterior surface, there meeting OD3–4, and extending laterally about half distance to distal end of Eb4, there meeting Ad5 dorsomedially; ventrally broadly on Cb5 posterolaterally; medially inseparable from SO. ② OP more or less divisible into lateral and medial sections.

Ad1–3 absent, moderately developed GFM1–3 present. ② GFM1 even more weakly developed than in *Gibbonsia*.

Ad4 dorsally narrowly on Eb4 ventrolaterally, continuing on Cb4 dorsolaterally medial to Eb4-Cb4 joint, fused broadly posteriorly with Ad5. (Not visible in illustrations.) ② Not fused with Ad5.

Ad5 dorsally on Eb4 posterolaterally, just attaching to posterodistalmost end of Cb4, ventrally on Cb5 dorsoposterodistally, there meeting PCI; anterior surface fuses with Ad4. ② Not fused with Ad4.

SOD broad.

RDs separated by distance less than one-fourth diameter one RD.

Additional remarks. SCL free from Bb3 (② attached mid-dorsally to posteroventral cartilaginous tip of Bb3). TV4 in two sections, dorsal portion divided and attached broadly to anterolateral surface of Cb5 on each side; ventral portion continuous across anterior ends of Cb5s. Pb1 cartilaginous; IAC, Pb2, Pb4 and UP4 absent. Eb1, Eb3, and Eb4 cartilage-tipped uncinat processes absent. Eb4 levator process absent.

CLINIDAE (CLININAE)

Heteroclinus perspicillatus (Valenciennes), USNM 201518, 110 mm SL.

Plate 191A, B

Additional material. ② = *Clinus acuminatus* (Bloch and Schneider), USNM 199579, 74.3 mm SL (Plate 191C); ③ = *Ophiclinus gracilis* (Waite), USNM 218794, 99.4 mm SL; ④ = *Springeratus xanthosoma* (Bleeker), USNM 204628, 68.9 mm SL.

Description.

Remarks. In general, only minor differences are exhibited by the four taxa.

LE1 on expanded bony dorsoposterior edge of Eb1 (no uncinat process).

LE2 very broad, on expanded bony dorsoposterior edge of Eb2.

LE3 very broad, on and lateral to all bony Eb3 uncinat process.

LE4 very broad but with much narrower insertion on Eb4 bony surface lateral to bony uncinat process, joining short raphe ventromedially with dorsomedial end of lateral section of OP. ② ③ Does not join OD3–4. ③ Just barely joins raphe with OP at Eb4 (see LP). ④ LE4 joins OD3–4 laterally, raphe with OP is just ventral to Eb4. ② Raphe with OP just ventral to Eb4, involves most of posterior edge of insertion.

LP on Eb4 at and slightly posterior to LE4 insertion, ventroposterolaterally joining raphe with dorsolateral end of OP lateral section. ③ Insertion anteriorly joins almost entire ventral edge of LE4 insertion, such that only medial edge of LE4 insertion joins OP, whereas entire posterior LP insertion joins raphe with OP.

LI1 on lateral edge and much of ventral surface of Pb3 anterior process (Pb2 absent).

LI2 on Pb3 dorsoposterolaterally medial to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 with broad anteromedial CT portion overlying surfaces of Pb3s anteriorly; muscular portion with mid-longitudinal raphe, which gives rise to CT sheets dorsally; muscular portion connected mid-ventrally between Pb3s to CT of pharyngeal roof, attaches laterally to dorsal surface of Eb2 at point opposite lateral end of LE2 insertion, joining fine raphe with dorsomedial end of GFM2, not connected posteriorly with TPb3-Eb4. TPb3-Eb4 on Pb3 dorsoposteriorly medial to LI2 insertion and on Eb4 medial end dorsoposteriorly, joined by diagonal muscle strand with SOD. ③ TEb2 relatively broad, covers all but anteriormost Pb3 surfaces.

OD3–4 origin on Pb3 dorsoposterolaterally ventral to TEb2, insertion on dorsoposterior surfaces of all bony Eb3 and Eb4 uncinat processes, joining raphe posteromedially with dorsomedial end of medial section of OP.

OP with posteriorly distinct lateral and medial sections; lateral section joining raphe dorsally with LE4 and LP insertions on Eb4, ventrally joining common raphe with ventroposterior end of Ad5, ventroposterolateral end of medial OP section, and dorsoanterior end of PCI; medial section dorsally on bony Eb4 uncinat process posteriorly, joining raphe medially with OD3–4, ventrally broadly on posterior surface of Cb5 impinging broadly on PCI attachment and ventrolaterally joining raphe with PCI, medially continuous with SO (continuation obscured in Plate 191A). ② ④ Two sections appear to be fused.

Ad1–3 absent (GFM1–3 weakly developed).

Ad4 (not visible in illustrations) dorsally on Eb4 anterolaterally ventral to LE4 insertion, ventrally continuing broadly onto distal one-third of Cb4 medial to Eb4-Cb4 joint.

Ad5 dorsally broadly on posterolateral edge of Cb4, passing mostly anterior to OP lateral portion, ventrally broadly on Cb5 dorsolaterally, joining common raphe posteroventrally with PCI dorsoanteriorly and OP lateral section ventrolaterally. ② Appears to be fused medially with OP, but should be verified in another specimen.

SOD present. ② ④ Absent. ③ Present.

RDs separated by narrow space. ③ Separated by space greater than diameter of one RD.

Additional remarks. SCL unusually thick, apparently continuous mid-dorsally with thick walls of aorta, which appears to be attached to ventroposterior surface of Bb3 (② ③ ④ SCL present). TV4 ventrally continuous between Cb4s, dorsally interrupted and attached to anterolateral surface of each Cb5. Pb1 cartilaginous; IAC, Pb2, Pb4 and UP4 absent. Cartilage tipped Eb1, Eb3, and Eb4 uncinat processes absent. Eb4 levator process absent.

LABRISOMIDAE

Calliclinus geniguttatus (Valenciennes), USNM 269371, 91.3 mm.

Plate 192

Additional material. ② = *Labrisomus philippi* (Steindachner), USNM 128206, 103 mm.

Description.

LE1 on expanded bony dorsoposterior margin of Eb1.

LE2 broadly on bony dorsoposterior edge of Eb2, ventroanterolateral edge joining raphe with TEb2 posterodistally.

LE3 on expanded bony dorsal edge of Eb3 dorsoanterodistally.

LE4 on most of bony dorsal surface of lateral half of Eb4, medial fibers joining raphe ventrally with presumed OP portion of fused Ad5 + OP + SO, ventrolaterally meets LP ventromedially. ② Joins raphe with medial section of OP dorsally.

LP on Eb4 meeting LE4 ventrolaterally; ventromedially joining CT with presumed Ad5 portion of Ad5 + OP + SO. ② Joins LE4 insertion posteriorly, not continuous with any other muscle.

LI1 on ventroanterolateralmost surface of Pb3.

LI2 on Pb3 dorsoposterolaterally just medial to medial end of Eb3.

TD comprises TEb2, TPb3-Eb4, and, vestigial TPb2. TPb2 (see discussion under Additional remarks) a fine, flat, semicircular ribbon of muscle on each side dorsal to TEb2; muscle originates anterolaterally on dorsoposterolateral edge of thick CT area

forming anteromedial area of TD and fuses with TEb2 anteromedially near posteromedial edge of CT. TEb2 anteriorly originates on posterior margin of CT area and is divided by mid-longitudinal raphe (CT area continuous anteriorly and ventrally with CT of pharyngeal roof, attaches also to medial end of Eb1, does not overlie Pb3, and gives rise dorsally to CT sheets covering TD); laterally, muscle attaches on Eb2 dorsally, reaching slightly anterolateral to LE2 insertion, almost to distal end of bony surface; muscle not continuous posteriorly with TPb3-Eb4. TPb3-Eb4 attaches mid-ventrally to CT of pharyngeal roof, laterally, broadly on Pb3 dorsally beginning anterior to LI2 insertion and continuing posteriorly, forming raphe with median edge of LI2 insertion, and continuing onto dorsodistal and posterodistal surfaces of Eb4. ② Lacks TPb2.

OD3-4 origin on Pb3 posterolaterally ventral to TEb2, insertion on dorsal edge of Eb3 that joins Eb4 and massively on Eb4 dorsally, with narrow section of fibers continuous posteroventrally with presumed OP portion of Ad5 + OP + SO.

OP fused indistinguishably with Ad5 medially and SO medially on right side, left-side Ad5 separate; ventrally, muscle complex joins raphe with PCI on Cb5. ② OP in two sections: medial section dorsally joining fibers of OD3-4 on Eb4 uncinat process; lateral section dorsolaterally on Eb4 ventral to LP insertion, dorsomedially continuous with LE4.

Ad1-3 absent (GFMs moderately developed).

Ad4 dorsally on Eb4 ventrolaterally, ventrally on dorsal surface of lateral quarter of Cb4, medial to Eb4-Cb4 joint, not visible in posterior view.

Ad5 fused indistinguishably with OP on one side, distinct on other: on Cb4 posterolaterally and Cb5 dorsodistally, partly anterior to OP. ② Distinct.

SOD absent.

RDs separated by space about one-half RD diameter.

Additional remarks. SCL attached mid-dorsoposteriorly by CT to ventroposterior end of Bb3 (cartilage tip not elongated). TV4 attached dorsally to anterolateral surfaces of Cb5s, continuous ventrally across Cb5s. Pb1 cartilaginous; IAC, Pb2, Pb4 and UP4 absent. Cartilage-tipped uncinat processes on Eb1, Eb3, and Eb4 absent. Eb4 levator process absent.

TPb2 is usually defined by its attachment to Pb2, which is absent in all blennioids. The muscle in *Calliclinus* is similar in shape and position to TPb2 found in some other acanthomorphs (e.g., *Dactyloptena*, Dactylopteridae; *Callionymus*, Callionymidae) and is undoubtedly vestigial, similar to its occurrence in *Rachycentron* (Plate 149) which has TPb2 weakly represented, present only unilaterally, and possibly anomalously.

Additional specimens of *Calliclinus* should be ex-

amined to verify presence of a vestigial TPb2. Presence of the muscle in our specimen may be anomalous. A specimen of the labrisomid genus *Auchenionchus*, which VGS considers a possibly plesiomorphic labrisomid, was not available for dissection and should also be examined. The presence of TPb2 in *Calliclinus*, probably has little bearing on the interrelationships of the blennioid families, although its presence in another labrisomid genus might indicate close relationship with *Calliclinus*.

CHAENOPSIDAE

Neoclinus blanchardi Girard, SIO 85-14, 129 mm.

Plate 193

Description.

LE1 broadly on anterior surface of all bony uncinat process of Eb1.

LE2 broadly on dorsoanterior surface of expanded bony flange of Eb2.

LE3 broadly dorsolaterally on Eb3 bony surface, joining Eb3 portion of OD3-4.

LE4 broadly on dorsodistal bony surface of Eb4, just encroaching on cartilaginous distal end.

LP on Eb4 posterior to LE4, fusing anteroventrally with LE4 insertion.

LI1 on lateral edge of Pb3 anterior process (Pb2 absent).

LI2 on Pb3 dorsoposterolaterally, just anterior to medial end of Eb3.

TD comprises TEb2 and TPb3-Eb4. TEb2 broad mid-dorsally, attenuated laterally, notched mid-anteriorly and mid-posteriorly, with mid-longitudinal raphe, which gives rise to CT sheets that attach to skull; broad mid-dorsal portion attached mid-anteroventrally to CT of pharyngeal roof and ventrolaterally to Pb3 dorsally; attenuated portion on Eb2 dorsally reaching point anteroventral to LE2 insertion; muscle overlapping anterior end of, and unattached to, TPb3-Eb4. TPb3-Eb4 broadly on Pb3 dorsal surface anterior to LI2 insertion, continuing posteriorly to point medial to insertion and onto Eb4 dorsomedially, continuous posteriorly with SOD.

OD3-4 origin broadly on Pb3 dorsally ventral to TEb2, insertion on Eb3 dorsomedially and dorso-medial edge of bony Eb4 uncinat process.

OP broadly dorsally on posterior surface of Eb4 extending from bony uncinat process laterally to point below LP insertion, ventrally on posterolateral bony surface of Cb5 dorsally, almost or partly meeting PCI, which attaches along much of posterolateral surface of Cb5 ventral to OP attachment and completely envelops distal end of Cb5.

Ad1-3 absent.

Ad4 beginning on ventral surface of Eb4 anterior to OP dorsally and extending to Eb4-Cb4 joint, and

attaching to dorsal surface of distal third of Cb4 medial to joint.

Ad5 on dorsal edge of Cb5 distally and much of posterolateral surface of Cb5; attachment includes posterodistalmost surfaces of Eb4 and Cb4.

SOD slender.

RDs unequal, well separated.

Additional remarks. SCL present, free from Bb3 cartilaginous posteroventral end (which has small, separate cartilage attached to tip). TV4 in two sections, dorsal portion divided and attached to antero-lateral surface of anterior end of Cb5 on each side; ventral portion continuous across anterior ends of Cb5s. Pb1 cartilaginous; IAC, Pb2, Pb4 and UP4 absent. Cartilage-tipped uncinat processes absent on Eb1, Eb3, and Eb4. Eb4 levator process absent.

Gobioidei

Remarks. Miller (1973), corroborated by Springer (1983), hypothesized the Rhyacichthyidae as the sister group of all other gobioids. Hoese and Gill (1993b) hypothesized Odontobutidae as the next gobioid clade, hence sister group to all remaining gobioids, but lacked a synapomorphy for the group. In additional remarks following the description of *Odontobutis*, we hypothesize a synapomorphy for the Odontobutidae. Recognition of family level taxa among the remaining gobioids is in a state of flux; our usage follows some generally recognized groups.

To the gobioid synapomorphies listed by Winterbottom (1993b) and Shibukawa et al. (2001), we add the absence of an Eb4 uncinat process, or, if a bony process is present, it lacks a cartilage tip. This character, however, occurs variously among other acanthomorphs. We have summarized a few other gill-arch character states for gobioids in Table 11.

Wang et al. (2001) based a molecular phylogeny of the gobioids on 32 genera belonging to six subfamilies in four different families. Our and their generic taxonomic coverages overlap very little, but one of their findings is, perhaps, supported by one of ours. Their strict consensus tree (their fig. 3) indicates a monophyletic grouping of their Sicydiinae (*Stiphodon*, *Sicyopterus*), Oxudercinae (*Periophthalmus*, *Boleophthalmus*), and some of their Gobionellinae genera (*Rhinogobius*, *Oligolepis*, *Stenogobius*).

Among the genera we examined, *Pseudapocryptes* (Oxudercinae) and *Sicydium* (Sicydiinae) are the only gobioids having the muscle, M. Pb3-Eb3. However, a similar muscle, M. Pb3-Eb3-Eb4, also occurs in *Gnatholepis* (the only member of the Gobionellinae we examined). These three genera also have a thick pad covering Pb3 dorsally. The muscle and pad perhaps offer support for Wang et al.'s (2001) findings and indicate a potentially new monophyletic group within the gobioids.

Table 11.—Distribution of certain characters in selected families and genera of gobioid fishes. P = present; – = absent.

Taxa	Characters											
	LI1 on	LI1 split	LI2 on	Pb4	UP4	TEb3	TEb4	TPb3	TPb3- Eb4	TPb3- Pb4	TPb3- UP4	TUP4
Rhyacichthyidae												
<i>Rhyacichthys</i>	Pb2 & Pb3	no	Pb3 & Pb4	P	P	-	-	-	P	-	-	-
Odontobutidae												
<i>Odontobutis</i>	Pb2 & Pb3	no	Pb3	P	P	P	P	P	-	-	-	-
<i>Micropercops</i>	Pb2 & Pb3	no	Pb3 (& Pb4 ?)	P	P	?	-	P	-	-	-	-
<i>Percottus</i>	Pb2 & Pb3	no	Pb3	P	P	P	-	P	-	-	-	-
Eleotridae												
<i>Eleotris</i>	Pb2 & Pb3	yes	Pb3 & Pb4	P	P	-	-	-	-	P	-	-
<i>Ophiocara</i>	Pb2 & Pb3	yes	Pb3 & Pb4	P	P	-	-	-	-	P	-	-
Microdesmidae												
<i>Microdesmus</i>	Pb2	no	Pb3	-	-	-	-	-	-	-	-	-
<i>Ptereleotris</i>	Pb2 & Pb3	no	Pb3 & UP4	-	P	-	-	P	-	-	-	P
<i>Nemateleotris</i>	Pb2 & Pb3	yes?	UP4	P	P	-	-	-	-	P	-	-
Xenisthmidae												
<i>Xenisthmus</i>	Pb2	no	Pb3	-	-	P	-	-	-	-	-	-
Gobiidae												
<i>Glossogobius</i>	Pb2 & Pb3	yes	Pb3 & UP4	-	-	-	-	P	-	-	-	-
<i>Bollmannia</i>	Pb2 & Pb3	yes	Pb3 & UP4	-	P	-	-	-	P	-	-	-
<i>Oxudercus</i> *	Pb2 & Pb3	yes	Pb3	-	P**	?	?	?	?	?	?	?
<i>Pseudapocryptes</i>	Pb2 & Pb3	yes	Pb3	-	P	-	-	P	-	-	-	P
<i>Gnatholepis</i>	Pb2 & Pb3	yes	Pb3	-	P	-	-	P	-	-	-	P
<i>Padogobius</i>	Pb2 & Pb3	no	Pb3	-	P	-	-	-	-	-	P	-
<i>Sicydium</i> *	Pb2 & Pb3	no	Pb3	-	P	-	P	-	-	-	-	-
<i>Trypauchen</i>	Pb2 & Pb3	no	Pb3	-	P	-	P	-	-	-	P	-

*Genus treated only incidentally in descriptive accounts.

**Apparently fused with UP3.

Another gobioid specialization, also present in a wide variety of percomorphs, is the Eb4 flange, a bony distal extension of Eb4 that overlaps the cartilaginous distal end of the element. Among the taxa we examined, its presence is variable among genera and even among individuals of the same species. In a cleared and stained specimen of *Rhyacichthys* (AMS 48695), the flange is well developed anteriorly on one side and absent on the other. In the illustrated specimen, the flange is weakly trilobed (anterior-middle-posterior) on one side and weakly bilobed (anterior-posterior) on the other, with the posteriormore lobe slightly better developed. In the odontobutids, it is only present anteriorly and varies from reduced to moderately developed. It is moderately developed anteriorly in eleotrids, weakly bilobed (*Ptereleotris*, *Nemateleotris*) or absent (*Microdesmus*) in microdesmids, well developed in (*Oxudercus*) or absent (*Pseudapocryptes*) among oxudercines, and absent in the generally reduced skeletons of xenisthmids and cerdalids. Among gobiids, it is well developed in *Gnatholepis* and *Padagobius*, well developed or absent in *Glossogobius*, and absent in *Bollmannia*. and *Trypauchen*.

RHYACICHTHYIDAE

Rhyacichthys aspro (Valenciennes), USNM 247300, 175 mm; QM I.31044, 165 mm.

Plate 194

Description.

LEI on dorsoposterior edge of Eb1 just lateral to base of uncinat process.

LE2 on dorsoposterolateralmost edge of Eb2, insertion impinges on TEb2 attachment.

LE3 on anterior surface of Eb3 just lateral to tip of uncinat process, insertion impinging medially on Eb3 insertion of OD3–4, and laterally on Ad3 attachment.

LE4 on dorsolateral end of Eb4, just meeting LP insertion.

LP on posterior edge of lateral end of Eb4.

LI1 on Pb2 uncinat process ventromedially and adjacent dorsoanterior edge of Pb3; posteriorly, insertion forms raphe ventromedially with anterolateral edge of OD3–4.

LI2 on Pb3 posterolaterally (at attachment of TPb3-Pb4 on Pb3) and on Pb4 dorsally.

Remarks. The insertion of LI2 on Pb4 occurs only

in gobioids among acanthomorphs (not all gobioids have Pb4).

TD comprises TEb2 and TPb3-Pb4. Anteriorly, TEb2 attaches broadly to CT of pharyngeal roof; muscle with mid-longitudinal raphe; anterolateral half of muscle crosses posterior half laterally and joins it, and together they attach broadly on Eb2 dorsally, almost reaching its lateralmost end. TPb3-Pb4 attaches broadly dorsolaterally on Pb3 and Pb4, including along entire medial line of LI2 insertion.

OD3-4 origin broadly on dorsoanterior bony surface of Pb3, insertion on joined uncinata processes of Eb3 and Eb4 (Eb4 process is all bony).

OP dorsally on posterior surface of Eb4, ventrally on posterior surface of Cb5.

Ad1 absent; GFM1 exceptionally well developed, on anterodistal surfaces of Eb1 and Cb1, distal edge attaching to gill filaments.

Ad2 well developed, comprising two layers, anterior layer (GFM) on distal half of Eb2 and dorsoanterior surface of Cb2, fibers running diagonally (ventrodistally), fusing with posterior layer (Ad) on anterodistal end of Eb2; fibers of posterior layer oriented almost vertically; distal edge of anterior layer attaching to gill filaments.

Ad3 comprising two layers similar to Ad2, except on Eb3 and Cb3.

Ad4 dorsally on dorsoposterior surface of Eb4, and ventrally on Cb4 medial to inner angle formed by Eb4-Cb4 joint.

Ad5 on posterodistalmost end of Cb4 and distalmost end of Cb5.

SOD broad.

RD well separated from contralateral element, inserts on Pb3 and, mostly, UP4.

Additional remarks. SCL free from Bb3 (cartilaginous posterior end not elongate or curved ventrally). TV4 free from Cb5s. Threadlike, cartilaginous Pb1 present as two or three linear segments, imbedded in CT and muscle of pharyngeal roof. Pb2 toothed. IAC present.

ODONTOBUTIDAE

Odontobutis obscura (Temminck and Schlegel), USNM 264892, 71.2 mm; USNM 264893, 2 specimens, 62.3-71.4 mm.

Plate 195

Additional material. ② = *Micropercops swinhonis* (Günther), USNM 336883, 56.6 mm; ③ = *Percottus glenii* Dybowski, USNM 105188, 63.9 mm. See also additional remarks for information on *Neodontobutis aurarmus* (Vidthayanon).

Description.

Remarks. We were unable to observe clearly the attachments of the posterior parts of the transversus

dorsalis and the insertion of LI2 in *Micropercops*. These attachments are much obscured by overlying muscles. In the case of LI2, the insertion joins a raphe with TD dorsal to an area where several crowded skeletal elements occur, all or only some of which might participate in the insertion. We indicate the attachments that we feel confident of, but further study is needed.

LE1 broadly, dorsally at and lateral to Eb1 uncinata process, reaching close to distal end of Eb1.

LE2 on Eb2 dorsoposteriorly, bordering TEb2 posterodistal margin.

LE3 on bony Eb3 uncinata process, bordering OD3 insertion posteriorly.

LE4 dorsodistally on bony surface of Eb4, insertion joined posteriorly with LP.

LP dorsodistally on Eb4, insertion joined anteriorly with LE4.

LI1 dorsally on joined anteriormost ends of Pb2 and Pb3, about same size as LI2.

LI2 on Pb3 dorsolaterally, passes between OD3 and OD3' on one side and OD3 and OD4 on the other on way ventrally from origin. ② Passes between OD3 and OD4 (OD3' absent); insertion joins raphe with TD medially and includes Pb3, at least (also possibly UP4 and Eb3; see remarks following description). ③ Passes through OD4 (OD3' absent) and inserts on Pb3 near joint with Pb4.

TD comprises TEb2, TPb3, TEb3, TEb4, with mid-longitudinal raphe coursing along TEb2, TEb3, and dorsoanterior half of TEb4. TEb2 broadly attached ventroanteriorly with CT of pharyngeal roof, anterior section twists as it extends laterally and joins remainder of muscle, which attaches on most of Eb2 dorsal surface; fascia attaches anterior surface of muscle to anterolateral end of Pb2 and IAC; muscle continuous posteriorly with TPb3. TPb3 extends anterolaterally and attaches to Pb3 ventral to TEb2 and OD4 and is continuous posteriorly with TEb3. TEb3 attaches to dorsomedial end of Eb3 and is posteriorly continuous with TEb4. TEb4 attaches to dorsomedial end of Eb4 and is weakly continuous mid-posteriorly with SOD. ② TD comprises TEb2 and at least TPb3, and attachments to Eb3 and UP4 may also be present (see remarks under description); TEb4 absent. ③ TEb4 absent.

OD3, OD3' origin on Pb3 laterally (sandwiched between Pb3 and Pb2) and extensively on Eb2 ventromedial surface, divides into dorsal (OD3) and ventral (OD3') portions distally; OD3 inserts on anterior surface of well-developed bony Eb3 uncinata process and OD3' inserts on anterodistal surface of Eb3 at medialmost point of attachment of Ad3. ② OD3 origin mainly on Pb3 dorsoposteriorly, with minor attachment to Pb2 dorsoposterolaterally; insertion on Eb3 dorsally at anterior edge of LE3 insertion; OD3' absent. ③ OD3 origin on Pb3 anterolaterally and Eb3

posteromedialmost end, insertion on Eb3 uncinat process; OD3' absent.

OD4 origin on Pb3 dorsoanteriorly ventral to TEb2, and slightly on dorsomedial end of Eb2 where it meets Pb3; divides into dorsal and ventral halves posterior to origin, insertion anteromedially on Eb4 dorsal surface. ② Insertion on Eb4 dorsoanteromedially, continuing onto ligament joining Eb3 at medial edge of LE3 insertion to Eb4 mid-posteriorly. ③ Origin on Pb3 with OD3, divides into dorsal and ventral portions by passage of LI2, portions recombine posterior to LI2 and insert on anterior surface of bony Eb4 uncinat process, meeting OD3 on Eb3 uncinat process.

OP dorsally on Eb4 ventroposterior margin posterior to main portion of Ad4, ventrally on posterodistal surface of Cb5 posterior to Ad5 attachment, medially inseparable from SO. ② ③ Distinct from SO medially.

Ad1 dorsally on anterolateral surface of Eb1, ventrally on anterolateral end of Cb1. ② Dorsally near end of anterolateral surface of Eb1. ③ On Eb1 anterior to LE1 insertion and on dorsoanteriormost surface of Cb1.

Ad2 short, on anterolateral ends of Eb2 and Cb2. ② On lateral third of Eb2 and anterodistal end of Cb2. ③ Meets ventrolateral edge of TEb2 and anterodistal end of Cb2.

Ad3 short, on anterolateral ends of Eb3 and Cb3. ② Extremely well developed, extends entire length of Eb3, but only on Cb3 anterolateralmost surface. ③ On most of Eb3 dorsal surface and anterolateral surface of Cb3.

Ad4 dorsally on distal half of Eb4 ventral surface, medially just anterior to dorsal attachment of OP, ventrally on Cb4 dorsoposterior margin just medial to inner angle of Eb4-Cb4 joint.

Ad5 dorsally on ventroposterior surface of Cb4, ventrally on posterodistalmost surface of Cb5 just anterior to ventral attachment of OP.

SOD present, continuous mid-anteriorly with TEb4.

RD juxtaposed to contralateral RD, inserts on Pb3 posterior margin and UP4 dorsally.

Additional remarks. SCL free from Bb3 (cartilaginous posterior end not elongated or curved ventrally. TV4 free from Cb5s. Pb1 present, cartilaginous. Pb4 and UP4 present. Pb2 toothed. Medial end of Eb4 larger than that of Eb3.

Some data were recorded for a paratype of *Odontobutis aurarmus* (recently assigned to the genus *Neodontobutis*, by Chen et al., 2002:233), USNM 325486, female, 37.1 mm, which has ambiguous affinities (Shibukawa et al., 2001:231): LI1 is on Pb2 and Pb3. LI2 divides OD4 into a large posterior section and a fine anterior section comprising a few muscle strands contiguous with OD3. TD comprises

TEb2 and, at least, TPb3 and TEb3 (we were unable to verify whether Pb4 is present, and whether there is an attachment to UP4). There is no TD attachment to Eb4. M. Pb2-Eb2, not present in the other gobioids we examined, is on Pb2, ventrolateral to the dorsoanterior cartilaginous tip, and Eb2 dorsoanterolaterally, there becoming continuous with TEb2 anterolaterally. OD3 originates ventrolateral to OD4 on Pb3 laterally and adjacent posteromedial edge of Eb3 and inserts anteriorly on bony support of uncinat process. OD4 originates on Pb3 dorsomedially and inserts on Eb4 bony uncinat process medial edge and anterior surface, with a few muscle strands on medial edge of Eb3 uncinat process. Pb1 is absent. SCL is free from Bb3. TV4 is free from Cb5s.

Hoese and Gill (1993:434) were unable to hypothesize a synapomorphy for the Odontobutidae, although they suggested, based on *Micropercops*, the possibility that a modification of the procurent caudal-fin cartilages might provide a synapomorphy. Watson (in Berra, 2001:460) indicated that "the morphology of procurent cartilages of *Odontobutis* and *Percottus* is unremarkable," thus implying that this potential specialization is not useful.

Akihito et al. (2000) provided results from a molecular based unrooted phylogenetic study of 28 gobioid taxa representing most of the gobioid families currently recognized based on morphological grounds. They found that the taxa grouped into eight groups: six clusters comprising two to eight taxa and a separate phyletic line each for *Odontobutis* and *Xenisthmus*. *Micropercops swinhonis*, the only other odontobutid included in their study, fell into a morphologically highly diverse group of six genera. They noted the morphological differences, shown by *Micropercops* compared with the other genera in its group, and the similarity of its morphology to that of *Odontobutis* and to that of their *Rhyacichthys-Protogobius* cluster. They indicated that more study was desirable to reconcile the conflicts, but concluded, nevertheless that their data did not support the composition (monophyly) of Hoese and Gill's (1993) Odontobutidae.

We find that the passage of LI2 through OD is unique to odontobutids, including *N. aurarmus*, among gobioids, and appears to satisfy the need for a synapomorphy that defines the Odontobutidae. It is possible the character is more widespread than recorded here, and it would be useful to determine if it is present in some other plesiomorphic gobioid genera of unresolved relationships, e.g., *Terateleotris* Shibukawa et al., *Protogobius* Watson and Pöllbauer.

Because of the variation in the position of LI2 within OD (whether separating the Eb3 from the Eb4 components, or splitting only the Eb4 component), it is possible that the position of LI2 vis-a-vis the OD

components is the chance result of individual ontogeny. A similar interposition of LI2 in OD3–4 also occurs, homoplastically in various ophiidiids, bythiids, and champsodontids, at least.

XENISTHMIIDAE

Xenisthmus sp., USNM 247389, 2 specimens, 29.2–33.3 mm.

Plate 196

Description.

Remarks. The gill arches are small and greatly depressed (almost flat) and the muscles are thin, unstained, and essentially transparent, making them difficult to interpret. The relationship of OP and SO are uncertain. Most of the description is based on the larger of the specimens.

LE1 on Eb1 at and just lateral to uncinat process.

LE2 absent.

Remarks. Muscle in position of LE2 is weakly, muscously attached to posterolateral end of Eb2, with muscous end continuing as fine tendon and inserting on distal end of Eb3. During cleaning, muscle invariably releases from Eb2, but maintains connection to Eb3.

LE3 present (see remarks under LE2).

LE4 dorsoanteriorly on distal end of Eb4.

LP just posterior to LE4 insertion (on Eb4–Cb4 joint on one side of larger specimen).

LI1 on Pb2 dorsolaterally.

LI2 on Pb3 dorsoposterolaterally.

TD comprises TEb2 and TEb3. TEb2 on mid-dorsoposterior edge of Eb2, continuous mid-posteriorly by diagonal muscle strap with TEb3, which is on mid-posterior edge of Eb3, continuous posteriorly by diagonal muscle strap with SOD.

OD3 absent.

OD4 origin broadly on Pb2 dorsoposteriorly and Pb3 dorsoanteriorly, insertion on Eb4 mid-anteriorly and on ligament joining Eb3 uncinat process with Eb4.

OP muscle fibers extending from most of posterior surface of Eb4 and attaching to Cb5, difficult to separate medially from SO (see remarks following description, above).

Remarks. Long, slender muscle strap (adventitious?) originates from SO and inserts on Eb4–Cb4 joint posteriorly on one side of larger specimen.

Ad1–2 absent.

Ad3 long, attaching along most of anterior surface of Eb3, but just reaching and attaching to Cb3 anterodistalmost surface.

Ad4 reduced, dorsally on Eb4 posterolaterally, ventrally on Cb4 dorsally anterior to inner angle of Eb4–Cb4 joint; dorsally just visible posteriorly lateral to OP.

Ad5 dorsally on Cb4 distally and Cb5 posterodistally.

SOD present, broad.

RD widely separated from contralateral RD, inserts by long tendon to posterior end of Pb3.

Additional remarks. SCL absent. TV4 free from Cb5s. Pb1 vestigial, minute and cartilaginous when present. Pb2 edentate. Pb4 absent; UP4 present, but reduced and entirely ventral to Eb4. IAC present.

Springer (1983:18–21; fig. 11) described and illustrated the osteology of *Xenisthmus clarus* (Jordan and Seale). The skeletal structure of the dorsal gill arches of the specimens in the present study is similar to that which Springer illustrated, except that the constricted medial end of the interarcual cartilage of *X. clarus* is present as a tiny autogenous cartilage. See also miscellaneous remarks under *Microdesmus*.

ELEOTRIDAE

Eleotris melanosoma Bleeker, USNM 321251, 3 specimens, 59.4–86.7 mm.

Plate 197

Additional material. ② = *Ophiocara porocephala* (Valenciennes), USNM 342613, 59.8 mm.

Description.

Remarks. Only conspicuous differences noted for *O. porocephala*.

LE1 broadly on Eb1 dorsal surface lateral to uncinat process.

LE2 broadly on Eb2 dorsoposteriorly, anterior edge of insertion along posterior edge of TEb2.

LE3 on Eb3, variably just lateral to tip of uncinat process or on and lateral to process.

LE4 tendinously on distal end of Eb4 dorsoanteriorly, joining LP insertion.

LP on dorsodistalmost surface of Eb4, anteromedially joining LE4 insertion.

LI1 anteriorly on dorsolateral surface of Pb2 ventral to LI1' insertion.

LI1' laterally on dorsoanterior edge of Pb3 dorsal to LI1 insertion.

LI2 on posterolateral dorsal surface of Pb3 and adjacent medialmost tip of Eb3, continuing uninterrupted onto lateral edge of Pb4. ② On Pb3 dorsolaterally and Pb4 laterally.

TD comprises TEb2 and TPb3–TPb4. TEb2 with mid-longitudinal raphe attaching ventrally to CT of pharyngeal roof, giving rise dorsally to filmy CT covering gill arches; flat ribbon of fibers arises from muscle anterolaterally, twists and extends laterally and inserts among fibers of remainder of TEb2, which extends onto Eb2 almost to dorsolateralmost end; muscle continuous mid-posteriorly with TPb3–Pb4. TPb3–Pb4 with mid-longitudinal raphe in Pb4 portion; muscle on Pb3 dorsoposterolaterally at me-

dial edge of LI2 insertion and on anterior margin of Pb4; muscle discontinuous (two specimens) or continuous by fine, diagonal muscle strand with SOD.

OD3 and OD4 with broad, continuous origin on dorsomedial surface of Pb3; muscle divides longitudinally into OD3 and OD4 after passing posteriorly from under TEb2; OD3 insertion on anterior surface of Eb3 uncinatate process and short ligament connecting Eb3 and Eb4 uncinatate processes. OD4 insertion on same ligament and Eb4 bony uncinatate process. ② OD3–4, indivisible.

OP with separate overlapping anterior and posterior layers, which may partially fuse in overlap area; anterior layer angled ventromedially from attachment to Eb4, attaches to Cb5 posteromedially; posterior layer angled ventrolaterally from attachment to Eb4 posteromedial surface, attaches ventrally on Cb5 posterolateral surface.

Ad1 dorsally on most of anterolateral surface of Eb1, ventrally on Cb1 anterodistalmost bony surface.

Ad2 dorsally on distal half of ventrolateral surface of Eb2; ventrally on anterior surface of distal end of Cb2.

Ad3 dorsally on most of dorsoanterior surface of Eb3, ventrally on anterodistalmost end of Cb3.

Ad4 dorsally on ventrolateral half of surface of Eb4, medially anterior to OP dorsal attachments; ventrally on dorsolateral surface of Cb4 anterior to inner angle formed by Eb4–Cb4 joint; separation from inner angle varying from little to noticeable.

Ad5 dorsally on posterolateralmost end of Cb4, ventrally on dorsolateral end of Cb5, meeting ventral attachment of posterior OP layer.

SOD present.

RD separated from counterpart by space less than half width of RD, tendinously attached to posterior end of Pb3.

Additional remarks. SCL present. TV4 free from Cb5s. Pb1 reduced, cartilaginous. Pb2 toothed. Pb4 and UP4 present. IAC present.

MICRODESMIDAE

Ptereleotris microlepis (Bleeker), USNM 257075, 78.0 mm.

Plate 198

Additional material. ② *Nemateleotris magnifica* Fowler, USNM 214103, 48.4 mm SL.

Description.

Remarks. The muscles of the two taxa are very similar in general appearance.

LE1 on Eb1 from lateral edge of uncinatate process to dorsodistal tip of Eb1. ② On Eb1 lateral to uncinatate process.

LE2 on Eb2 dorsodistally.

LE3 finely, tendinously on Eb3 lateral to uncinatate process.

LE4 finely, tendinously on dorsodistal end of Eb4. LP at and posterolateral to LE4 insertion.

LI1 broadly, dorsoanteriorly on Pb2 and Pb3. ② Same, but easily divisible (artificially?) into two muscles, one on each of the skeletal elements.

LI2 very broadly on Pb3 posterolaterally and UP4 medially (Pb4 absent), easily divisible (artificially?) into two muscles, one on each of the skeletal elements. ② On UP4 dorsally lateral to small Pb4, muscle not obviously divisible.

Remarks. ② Absence of insertion on Pb3 and Pb4 noteworthy.

TD comprises TEb2, TPb3, and TUP4. TEb2 deeply notched anteriorly, notch dividing broad anterior portion of muscle into right and left halves, each of which originates on CT pad conforming with dorsomedial surface of Pb3; posterior portion of muscle broad, transversely continuous with mid-longitudinal raphe continuing posteriorly from anterior notch; both sections extend laterally, with posterior section attaching to posterior edge of Eb2 and dorsal section twisting and overlapping posterior section and attaching to dorsal surface of Eb2; TEb2 ending posteriorly as CT, which is continuous mid-posteroventrally with mid-longitudinal raphe of TPb3. TPb3 attaches to Pb3 laterally, anteriorly meeting medial edge of LI2 insertion on Pb3 (unclear if some TPb3 fibers also attach to UP4), mid-posteriorly continuous with raphe of TUP4. TUP4 somewhat asymmetrical, attaching to UP4 posteromedially, continuous mid-posteriorly with median raphe of SOD. ② Comprises TEb2 and TPb3–Pb4. TEb2 similar to *Ptereleotris*, but “dorsal” section not clearly overlapping posterior section (therefore, not dorsal). TPb3–Pb4 dorsolaterally on Pb3 just medial to cartilage tip of process articulating with medial end of Eb3 and on medialmost edge of small Pb4.

OD3–4 broadly on Pb3 dorsomedially ventral to TEb2, insertion on Eb3 uncinatate process and Eb4 mid-dorsolaterally (no uncinatate process). ② OD origin narrowly anteriorly on Pb2 and broadly posteriorly on Pb3, divides into OD3 and OD4 shortly after passing posteriorly from under TD; OD3 inserts on Eb3 uncinatate process and OD4 inserts on Eb4 mid-dorsolaterally (no uncinatate process).

OP on Eb4 dorsoposteriorly; ventrally, narrowly on Cb5 anterodistalmost surface.

Ad1–3 broadly on anterior surface of respective Eb, and less extensively on associated Cb; Ad1 overlain anteriorly by broad bases of two dorsalmost gill rakers.

Ad4 almost completely overlapped posteriorly by OP; dorsally, broadly on Eb4 ventral surface; ventrally, narrowly on Cb4 anterior to internal angle of Eb4–Cb4 joint.

Ad5 dorsally on Cb4 posterodistal end, ventrally on Cb5 distally.

SOD present.

RD separated from counterpart by interspace equal to about half width of RD, inserts on Pb3 posteriorly.

Additional remarks. SCL present, free from Bb3 (cartilaginous posterior elongate, not extended ventrally). TV4 free from Cb5s. IAC present. Pb1 questionably present, but possibly the separate rod-like cartilage at the tip of Eb1 anterior process represents a segmentation near the base of the cartilaginous end of the anterior process, which is often unusually long in gobies. Pb4 absent, UP4 present. ② Eb1 with elongate cartilaginous tip, no separate Pb1, Pb4 and UP4 present. Pb2 toothed.

Microdesmus longipinnis (Weymouth), USNM 199614, 162 mm.

Plate 199

Description.

LE1 on Eb1 dorsally lateral to uncinat process.

LE2 on Eb2 dorsodistally.

LE3 slender, on Eb3 just dorsolateral to bony uncinat process.

LE4 very fine, inserts by short, fine tendon on Eb4 dorsodistally at medial edge of LP insertion.

LP much broader than LE4, on distalmost end of Eb4.

LI1 on dorsomedial surface of Pb2.

Remarks. Pb2 posterior end abuts Pb3 anterior end. Except for xenisthmids (Springer, 1983:fig. 11, *Xenisthmus*; Gill, 1993:fig. 6, *Paraxenisthmus*) schindleriids (Johnson and Brothers, 1993:fig. 8), and *Microdesmus*, the anterior portion of the gobioid Pb3 lies dorsal to Pb2, and LI1 (or LI1 + LI1') inserts on both Pb2 and Pb3. LI1 is also only on Pb2 in *Xenisthmus*, which does not have LI1', which is possibly present in the least specialized xenisthmid, *Paraxenisthmus* (condition in *Schindleria* also unknown). Although the alignment of Pb2 and Pb3 in these families may be attributable to developmental truncation of the head (the species are small and/or have small heads), Pb2 and Pb3 retain their dorsal-ventral relationship in the gobiid genus *Eviota* (levators not studied), one of a few gobioid genera that include some of the smallest fish species.

LI2 on Pb3 dorsoposterolaterally.

TD comprises only TEb2, which attaches broadly along Eb2 posteriorly and is mid-posteriorly continuous by a fine muscle strand with SOD.

OD3–4 arises broadly along medial edges of Pb2 and Pb3 and inserts dorsoanteriorly on bony Eb3 uncinat process and on Eb4 mid-dorsally, joining raphe with OP; posteriorly partly continuous with dorsal attachment of OP.

OP dorsally with two separate attachments on Eb4; lateral attachment joining raphe with OD3–4, medial attachment posteromedially on Eb4; ventrally on Cb5 dorsodistally at and posterior to ventral attachment of Ad5.

Ad1–3 on respective Eb near medial end, mostly free from shaft, and on respective Cb anteriorly near distal end.

Ad4 on Eb4 ventrodistally and Cb4 dorsally medial to Eb4-Cb4 joint.

Ad5 dorsally on Cb4 dorsodistally, ventrally on Cb5 dorsodistally.

SOD unusually broad.

RD separate slightly from counterpart, inserting on Pb3 medially and posteriorly.

Remarks. The RDs enter the esophagus well posterior to gill arches.

Additional remarks. SCL present. TV4 free from Cb5s. Pb1 absent Pb2 minutely toothed. Pb4 and UP4 absent. IAC absent.

GOBIIDAE

Pseudapocryptes elongatus (Cuvier), USNM 341281, 137 mm.

Plate 200

Description.

LE1 on Eb1 dorsolateral surface beginning at base of uncinat process and extending to end of bone.

LE2 on dorsolateral one-third of surface of Eb2.

LE3 in two sections dorsal to insertion; inserts by tendon bridging dorsomedial edge of uncinat process and dorsolateral surface of Eb3.

LE4 slender, tendinously attached to Eb4 dorsodistally just anterior to lateral edge of LP insertion.

LP broad based, insertion covering almost all of bony Eb4 surface distal to uncinat process.

LI1 on Pb2 dorsally ventral to dorsomedial cartilage-tipped process.

LI1' completely separate from LI1, on Pb3 dorsally near anteromedial end.

Remarks. LI1' also occurs in *Gnatholepis*, *Bollmannia*, *Glossogobius*, *Eleotris*, and *Ophiocara*.

LI2 on Pb3 dorsoposteromedially ventral to OD3–4 origin (Pb4 absent; UP4 present).

TD complex, all elements either completely separated medially or joined by broad CT area, comprises TEb2a, TEb2p, TPb3, TUP4, and TD median fibers that overlie the broad CT area. The CT area appears to be an expansion of the normal median raphe that occurs in the TD of other gobies. TD median fibers originate as complex web of fine fibers mid-dorsally on CT area between TEb2p and give rise to a slender longitudinal muscle on each side that inserts on the CT pad on which TEb2a originates. TEb2a origin dorsally on spongy CT pad dorsal to Pb3 anteriorly, insertion on Eb2 dorsally just proximal to medial

edge of LE2 insertion, a few fibers attaching to tendinous insertion of TEb2p, completely separate from contralateral TEb2a. TEb2p origin as multiple slender muscle straps on mid-dorsal CT section, insertion tendinous on Eb2 ventromedial to TEb2a insertion. TPb3 origin on mid-dorsal CT area, insertion on Pb3 dorsoposterolaterally just medial to medial end of Eb3. TUP4 origin on mid-dorsal CT area, insertion on medial edge of UP4.

Remarks. TEb2a & p appear to be a specialized separation into two parts of the typical gobioid TEb2, which comprises two incompletely separate sections laterally.

M. Pb3-Eb3 origin on Pb3 dorsoposteriorly, insertion on Eb3 dorsoposterodistally.

OD3 and OD4 originate broadly from mixed fibers attaching to Pb3 dorsomedial edge ventral to TEb2p, but are distinct muscles for almost all of their lengths. OD3 is divided mid-longitudinally dorsally, but fibers of two sections mesh ventrally, muscle inserts tendinously to medial edge of Eb3 uncinat process. OD4 inserts on dorsoanteriormost edge of Eb4 just anterior to bony Eb4 uncinat process.

OP dorsally on Eb4 ventrally posterior to lateral portion of Ad4, ventrally, finely, tendinously on edge of Cb5 at attachment of Ad5.

Ad1 dorsally on almost entire anterior surface of Eb1 medial to uncinat process, ventrally on Cb1 broadly anteriorly medial to cartilaginous distal end.

Ad2 dorsally on bony anterior edge of Eb2 laterally, ventrally on anterior surface of distal bony and cartilaginous end of Cb2 medial to Eb2-Cb2 joint.

Ad3 dorsally on bony anterior edge of Eb3 anteroventral to uncinat process, ventrally on anterior surface of cartilaginous distal end of Cb3 ventral to Eb3-Cb3 joint.

Ad4 in two separate sections. Anterior section originates on Eb4 dorsally anterior to posterior section and inserts finely on Cb4 dorsal edge just medial to Eb4-Cb4 joint; posterior section originates on Eb4 dorsally posterior to origin of anterior section and inserts narrowly on Cb4 near lateral end of insertion of anterior section.

Ad5 on cartilaginous Cb4 posterodistal end and distally on broad, distal cartilaginous edge Cb5.

SOD absent.

RDs separated by narrow space anterior to origins, each divides anteriorly into lateral section consisting of loose fibers that insert on posterior edge of UP4, and median robust section that inserts along medial edge of Pb3.

Additional remarks. SCL free from Bb3 (cartilaginous posterior end not elongate or extended ventrally). TV4 in two parts: posterior part, narrow, continuous, and free across ventral surfaces of Cb5s; broad anterior part on each side attaching medianly

to ventral surface of cartilaginous anterior ends of Cb5s. Pb1 absent. Pb2 toothed. IAC absent.

Glossogobius aureus Akihito and Meguro, USNM 241833, 2 specimens, 81.4–117 mm.

Plate 201

Additional material. ② = *Bollmannia chlamydes* Jordan, 71.5 mm.

Plate 202

Additional material. ③ = *Padogobius nigricans* (Canestrini), 70.2 mm.

Description.

LE1 mid-dorsally on Eb1 just lateral to uncinat process. ③ On distalmost bony surface of Eb1.

LE2 mid-dorsally on Eb2 just lateral to bony process on posterior edge. ③ Broadly on Eb2 beginning at distalmost end and extending medially.

LE3 on Eb3 just lateral to tip of uncinat process. ③ On lateral edge of tip of uncinat process and extending a short distance laterally.

LE4 on dorsodistalmost bony end of Eb4.

LP at and posterior to insertion of LE4. ③ Fusing with LE4 laterally just dorsal to LE4 insertion.

LI1 on Pb2 dorsoanteriorly. ③ On Pb2 and Pb3 dorsoanteriorly.

LI1' on Pb3 dorsoanteriorly just posterior to LI1. ③ Absent.

LI2 in larger specimen on Pb3 dorsal surface posterolaterally and UP4 anterolaterally, in smaller specimen also on tiny Pb4 (Pb4 probably anomalous, not present in larger specimen or ② and ③). ③ On Pb3 dorsoposterolaterally with few strands on Eb3 dorsomedialmost surface.

TD comprises TEb2 and TPb3. TEb2 broad with median longitudinal raphe on posterior half in larger specimen (complete in smaller specimen; apparent pair of raphes anteriorly in larger specimen are artifacts), raphe continues posteriorly across TPb3 and SOD; muscle twists and divides laterally with posterior portion of muscle passing anteroventral to anterior portion and attaching to hook-like process (not illustrated) on mid-anterior edge of Eb2; anterior portion attaches to Eb2 anterior surface just posterior to hooklike process; posteriorly broadly continuous with TPb3. TPb3 originates from posterior half of median raphe, passes laterally ventral to OD3 and OD4 and attaches to Pb3 dorsally medial to LI2 insertion. TPb3 narrowly continuous mid-posteriorly with SOD at median raphe.

② TD comprises TEb2 and TPb3-Eb4, mid-longitudinal raphe like *Glossogobius*. TEb2 similar to *Glossogobius*, but no hooklike process on Eb2. TPb3-Eb4 on Pb3 dorsoposterolaterally immediately anterior to medial end of Eb4, continuing onto medial end of Eb4 dorsally.

③ TD comprises TEb2 and TPb3-UP4; median raphe restricted to posterior portion of TEb2, continuing across TEb3-UP4, and only anterior half of SOD; TEb2 twist not apparent, extending laterally to, and joining medial edge of LE2 insertion and joining raphe with Ad2 dorsally (no hook-like process on Eb2); continuous broadly posteriorly with TPb3-UP4. TPb3-UP4 on Pb3 dorsoposteriorly medial to medial end of Eb4, continuing onto UP4 dorsally just posteroventral to medial end of Eb4, broadly continuous posteriorly with SOD.

OD3 and OD4 originate inseparably on dorsomedial surface of Pb3 ventral to TEb2; muscle divides into OD3 and OD4 as it passes out from under TEb2, with OD3 inserting on dorsomedial edge of Eb3 uncinat process and OD4 inserting on dorsomedial edge of bony Eb4 uncinat process. ③ OD3-4 present, not separable into two muscles.

OD4 (see OD3 above).

OP dorsally broadly on Eb4 posterior surface extending medially almost to medial end, ventrally on posterolateral surface of Cb5 posterior to Ad5 attachment.

Ad1 dorsally on most of bony length of Eb1 ventrally, ventrally on anterodistalmost surface of Cb1 (muscle does not pass anterior to cartilaginous distal end).

Ad2 dorsally on ventral bony surface of Eb2 beginning at mid-anterior hooklike process (anteroventral to LE2 insertion) and extending laterally to end of bone, ventrally on anterodistal surface of Cb2 (muscle does not pass anterior to cartilaginous distal end). ② Dorsally begins at mid-length of Eb2 (no hooklike process). ③ Dorsally on ventral surface of Eb2 well medial to LE2 insertion, forming raphe dorsally with anterior edge of Eb2 portion of TEb2.

Ad3 dorsally on most of bony surface of Eb3, ventrally on anterodistal surface of Cb3 (muscle does not pass anterior to cartilaginous end); section of fibers arises dorsoposterolaterally from main muscle mass and attaches to anterior surface of uncinat process ventral to OD3 (in frontal view, Ad3 appears to be two muscles, more-or-less horizontal anterior portion overlapping posterior vertical portion). ③ Vertical section smaller, inconspicuous, inclined dorsomedially, only on posterolateral surface of uncinat process.

Ad4 dorsally broadly on Eb4 ventrally anterior to OP, ventrally broadly on Cb4 dorsal surface medial to Eb4-Cb4 joint.

Ad5 dorsally beginning on posterodistal end of Cb4 and extending medially short distance, ventrally to anterodistal end of Cb5 and extending short distance medially anterior to OP attachment.

RDs slightly separated. ② Adjacent.

SOD slender, connected at mid-dorsal raphe with TPb3. ③ SOD broad.

Additional remarks. SCL free from Bb3. TV4 free from Cb5s. Pb1 absent. Pb2 toothed. IAC present.

Trypauchen vagina (Bloch and Schneider), USNM 339608, 149 mm.

Plate 203

Description.

LE1 on Eb1 dorsolateralmost bony surface.

LE2 on Eb2 dorsolateralmost bony surface, meets dorsal attachment of Ad2 and distal edge of TEb2.

LE3 on Eb3 just lateral to tip of uncinat process.

LE4 on Eb4 dorsally near distal end, joins LP insertion laterally.

LP on dorsodistal end of Eb4 at and lateral to LE4 insertion.

LI1 on Pb2 dorsoanteriorly and adjacent anterior end of Pb3, not divisible.

LI2 inserts by broad tendon posterolaterally on Pb3 dorsal surface.

TD comprises TEb2, TPb3-UP4, and TEb4. TEb2 attached broadly anteroventrally and ventrally from mid-longitudinal raphe to CT of pharyngeal roof (raphe continues across TPb3-UP4); on left side only, thin, medially concave slip of muscle arises from main muscle mass anterolaterally and re-enters posterolaterally; thin, flat muscle slips extend posterolaterally and laterally from mid-longitudinal raphe and join as lateral arm of TEb2 attaches to Eb2 dorsal surface; broadly continuous posteriorly with TPb3-UP4. TPb3-UP4 attaches to Pb3 posteromedially and UP4 dorsally, and is continuous posteriorly with TEb4. TEb4 attaches to Eb4 mid-posteriorly and lies dorsal to SOD.

OD3 and OD4 superficially completely fused, but actually almost completely separate except for fine line of fusion ventrally; muscles originate broadly along Pb3 dorsal surface; OD3 inserts along dorsoanterior surface of Eb3 uncinat process and anterior portion of tight ligament connecting Eb3 and bony Eb4 uncinat processes; OD4 inserts on ligament and dorsomedial edge of Eb4 uncinat process.

OP dorsally on dorsoposterior surface of Eb4, ventrally on Cb5 posterodistally, meeting Ad5 ventral attachment; posteriorly, broadly overlaps Ad4 dorsal attachment on ventral surface of Eb4.

Ad1 on most of length of anterior edge of Eb1 and on anterolateral surface of Cb1.

Ad2 broadly on Eb2, forming raphes with ventrolateral edge of TEb2 and ventromedial edge of LE1, ventrally on anterolateral surface of Cb2.

Ad3 dorsally on most of anterolateral edge of Eb3, ventrally on anterolateral surface of Cb3.

Ad4 dorsally broadly on Eb4 ventral surface, mostly occluded in posterior view by posteriorly

overlying OP, ventrally on Cb4 dorsolateral surface medial to inner angle formed by Eb4-Cb4 joint.

Ad5 dorsally on posterodistal end of Cb4, ventrally on Cb5, meeting OP ventral attachment.

RDs contiguous, inserting on Pb3 and UP4 posteriorly; right side RD with anomalous fibers branching off ventral surface posterior to level of SOD and meshing with SO fibers.

SOD present.

Additional remarks. SCL present (condition precluded observing if it was free or attached to Bb3. TV4 free from Cb5s. Pb1 and Pb4 absent, UP4 present. Pb2 toothed. IAC present, reduced.

Gnatholepis cauerensis (Bleeker), USNM 327750, 2 specimens, 42.4–45.6 mm.

Plate 204

Description.

LE1 dorsolaterally on Eb1 beginning at base of uncinat process.

LE2 on Eb2 dorsally near distal end.

LE3 on dorsal edge of Eb3 between tip of uncinat process and distal end of Eb3.

LE4 on Eb4 dorsally near distal end.

LP massive, broadly on Eb4 dorsally, lateralmost end at and posterior to LE4 insertion, inserted posterolaterally on dorsal end of ligament joining Eb4 and Cb5.

LI1 on Pb2 anterolaterally ventral to TEb2 anteriormost section.

LI1' on Pb3 anterolateralmost end ventral to TEb2 anteriormost section; insertion separated by space from LI1 insertion; LI1 and LI1' appearing as one muscle after extending out from under TEb2.

LI2 on Pb3 dorsomedial surface near cartilaginous process that articulates with medial cartilage tip of Eb4.

TD comprises TEb2 and TPb3. TEb2 comprises three, almost completely separated sections; anterior two sections originate on and are broadly interrupted medially by CT pad over dorsal surface of Pb2 and anterior surface of Pb3; interrupted sections divide as they extend laterally, posterior section twisting and becoming ventral to anterior section before attaching on posteroventral edge of Eb2 well medial to distal end; anterior section attaches on dorsal surface of Eb2 just medial to LE2 insertion; uninterrupted posteriormost section of TEb2 with median longitudinal raphe, muscle continuous mid-posteriorly with CT sheet covering dorsoposteriormost surfaces of Pb3s; as posteriormost section of TEb2 extends laterally, it joins posterior interrupted TEb2 section. TPb3 originates from all margins except anteriormost of CT sheet covering Pb3 dorsoposterior surfaces and attaches on Pb3 dorsoposterolaterally near process that

articulates with Eb4; TPb3 is narrowly continuous mid-posteriorly with SOD.

M. Pb3-Eb3-Eb4, slender muscle originating mostly on anterior surface of Pb3 process that articulates with Eb4 and dorsally on medial cartilaginous tip of Eb4, extends laterally at right angles to long axis of gill arches and inserts on posterior surface of Eb3 ventral to tip of uncinat process.

OD3 originates ventral to TEb2 on mid-lateral edge of anterior Pb3 articulating surface and at and ventral to OD4 origin, and inserts on Eb3 uncinat process.

OD4 originates ventral to TEb3 on mid-lateral edge of anterior Pb3 articulating surface and at and dorsal to OD3 origin, and inserts anteriorly on mid-dorsal flat, bony Eb4 uncinat process.

OP broadly dorsally on Eb4 posteriorly and ventrally on broad ligament joining LP and Eb4 to Cb5; completely obscures Ad4 from posterior view.

Ad1 on Eb1 bony anterior surface, extending from medialmost end to medial edge of LE1, there crossing ventrally and attaching on anterior surface of distal end of Cb1.

Ad2 on bony process on anterior edge of Eb2 and on anterior surface of cartilaginous end of Cb2.

Ad3 on ventral edge of distal bony half of Eb3 and anterior surface of cartilaginous end of Cb3 (not visible in illustration).

Ad4 dorsally on ventral edge of Eb3, ventrally narrowly on Cb4 dorsally medial to Eb4-Cb4 joint; completely occluded from external view.

Ad5 short, dorsally on Cb4 posterodistally and Cb5 posterodistalmost end.

SOD slender.

RDs paired on each side, ventral member of pair slightly separated from counterpart, inserts on posterior margin of Pb3; dorsal member of pair well separated from counterpart, inserts mostly on posterior end of UP4 with few medial fibers attaching to Pb3 together with lateralmost fibers of ventral member.

Additional remarks. SCL free from Bb3 (cartilaginous posterior end not elongate or extending ventrally). TV4 free from Cb5s. Pb1 absent. Pb2 toothed. IAC present.

Pleuronectiformes

PSETTODIDAE

Psettodes erumei (Bloch and Schneider), USNM 366443, 106 mm, eyes on left side.

Plates 205.1, 205.2

Description.

LE1 on Eb1 dorsally at base of uncinat process.

LE2 on expanded dorsal edge of Eb2 at about mid-length.

LE3 absent.

LE4 on posteroventral surface of Eb4 uncinat process.

LP slender, fragile filament on Eb4 at lateral edge of LE4 insertion.

LI1 on Pb2 dorsoanteriorly; anteromedially joining moderately long raphe with TPb2 laterally.

LI2 broadly on lateral edge of Pb3 posteriorly.

TD comprises TPb2, TEb2, and TEb4. TPb2 attaches muscously dorsoanteriorly to Pb2 dorsoanteriorly, and tendinously anterolaterally to Pb1 ventrolaterally and Eb1 dorsoanterolaterally (attachment to Pb1 and Eb1 unknown in other fishes); right-side portion of TPb2 folds over left side posteriorly, and medial edge is interrupted by raphe that gives rise to CT sheet that attaches to cranium; posterolaterally, on each side, TPb2 joins another raphe with TEb2, and muscle strands extend posteromedially from raphe of each side and become continuous with TEb4 posteromedially. TEb2 attaches laterally along most of anterior edge of Eb2 medial to raised dorsal Eb2 margin and LE2 insertion. TEb4 attaches mid-ventrally by CT among longitudinal fibers of long, strap-like muscle extension of SO (extension attaches to Pb3 anteromedially); TEb4 ventrally continuous by muscle filaments with SOD anteriorly.

OD3–4 origin on dorsoanterior surface of Pb3; in-

sertion on Eb3 dorsoanteriorly and, beginning on medial edge of Eb4 uncinat process and continuing past Eb3 uncinat process, attaching broadly on Eb4 anteriorly ventral to uncinat process.

OP in medial and lateral sections. Medial section dorsally on Eb4 posteromedial to uncinat process; lateral section dorsally on Eb4 posteriorly ventral to LE4 insertion; medial section attaches ventrally to hook-like process on Cb5 mid-posteriorly (not visible in illustrations) and to adjacent arm of Cb5, overlapping posteriorly and continuous with lateral OP section, which is on Cb5 dorsolaterally between attachments of TV5 and Ad5.

Ad1–3 absent.

Ad4 broadly dorsally on Eb4 lateral to LE4 insertion, ventrally, not so broadly on Cb4 slightly medial to Eb4-Cb4 joint.

Ad5 anteriorly on posterodistal ends of Eb4 and Cb4, posteriorly on Cb5 anterodistally.

SOD present.

RDs adjacent, insert on posteromedial surface of Pb3 and anteromedial edge of UP4.

Additional remarks. SCL attached mid-dorsally to elongate cartilaginous posteroventral tip of Bb3. TV4 free from Cb5s. Pb4 absent, UP4 present. Pb2 toothed. IAC present. Eb4 levator process absent.

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APPENDIX

Phylogenetic analysis of the families of acanthomorph fishes based on dorsal gill-arch muscles and skeleton

Victor G. Springer and Thomas M. Orrell

"The unraveling of phyletic lines within the Perciformes is made difficult by the sheer number of species and genera. One is faced with the choice of mining a narrow vein for nuggets of knowledge which lie isolated, or engaging in a strip mining operation which reveals broad patterns at the expense of ignoring contradictory details."

Richard H. Rosenblatt (1984).

Introduction

This section comprises a phylogenetic analysis of the Acanthomorpha based almost exclusively on gill-arch muscle and skeletal characters examined and described in the Springer and Johnson (henceforth, S&J) portion of this study. The analysis includes 168 individual taxonomic groups (Table 12) comprising 147 families out of a total of approximately 250 acanthomorph families and 2400 genera (increased arbitrarily based on Nelson's 1994:253, figures). Of these, 15 families in the analysis are represented by multiple taxa (e.g., all four genera of Polycentridae; three different genera of Labridae), and 132 families are represented individually. The individually represented families include either all the taxa S&J examined for the family (see the pertinent family accounts), which might be several genera and species, or a single genus and all its examined species, which might only be one (e.g., Cichlidae, *Ptychochromis*). In the latter case, the generic name follows the family name on the cladograms (Figs. 5 and 6). The reasons for selecting a single taxon, as opposed to all that were examined, varied. Usually, the single taxon was chosen because a published study or colleague indicated that it was the basal member, or among the more basal members, of the family group that S&J examined. For example, of the six gobioid families treated in the descriptive accounts, only Rhyacichthyidae are entered in the matrix, based on: Miller (1973), Springer (1983), and Hoese and Gill (1993). For Opistognathidae, *Lonchopisthus*, was suggested by W.F. Smith-Vaniz (pers. comm.). In other cases we selected taxa that might include a relatively unspecialized taxon in a group for which a basal member has not been hypothesized (e.g., Labridae, Ambassidae).

Fifty-six characters (1–36, 36a, 37–55), comprising 137 character states, were used in preparing Table 12. Characters 1–36a refer to gill-arch muscles, 37–55 are osteological, mostly gill-arch skeletal characters examined during the descriptive part of the study. Character 36a was added after all other characters had been coded and rather than re-number characters 37–55, we chose to interpolate the additional character as 36a.

S&J described character 36 for many, but not all, taxa. The character was observed in the remaining taxa and coded directly into the matrix. Similarly, S&J did not describe character 43 in any taxa. Because it pertains to the dorsal gill arches, and was noticed during the study, the character was examined for all taxa for the Appendix and coded directly into the matrix.

Character states were coded based on the states in *Synagrops* (Acropomatidae), a relatively unspecialized percomorph, because it was initially intended to analyze only percomorphs. Non-percomorphs were added and rather than re-code based on a non-percomorph we continued to code based on *Synagrops*.

Character 53 is the single synapomorphy Johnson and Patterson (1993) used to hypothesize their Smegmamorpha. We did not verify the character states for character 53 in our study, but infer them from Johnson and Patterson (1993). We added this character in order to enable a stronger test of the monophyly of the Smegmamorpha.

Among acanthomorphs, character 55 is a unique synapomorphy of the Anabantomorpha and character 54 is confined to the Anabantoidei. We added these two characters in an attempt to restrict the anabantomorph taxa included in the analysis.

Parsimony Analysis

A PAUP NEXUS file was developed from the characters described below. The file contained PAUP commands and a matrix of 168 taxa by 56 characters, or 9408 cells. Multi-state characters were assigned single symbols using the PAUP "equate" function. Although character states were coded based on *Synagrops* (Acropomatidae), characters were not ordered and were given equal weight for the parsimony analysis because of the large number and diversity of taxa involved. Each of the 56 characters was informative under parsimony. States were unknown or inapplicable for several characters. Both states are treated as "missing" by the parsimony algorithm, because under the algorithm there is no way to differentiate between them (Swofford 2003). Characters with missing data do not affect the placement of taxa on the tree. Trees were mid-point rooted. This method

of tree drawing roots at the midpoint of the longest path linking any pair of taxa. Functionally, this produces a tree that is not explicitly rooted. However, the use of this option in PAUP* forces MINF re-optimization of the tree (the only optimization method which is not dependant on root position).

Parsimony analyses were conducted using PAUP* version 4.0b10 (Swofford 2003) and were run on an Alpha 64 bit processor running RedHat Linux version 7.1 Alpha. The analysis was run with the following parameters: starting trees obtained via stepwise addition; swapping algorithm tree bisection-reconnection; no topological restraints; all trees unrooted; character-state optimization accelerated transformations (MINF optimization was used to draw trees); MulTrees option in effect; starting seed = 524970930; heuristic search of 1000 random addition replicates with 10 trees held at each step during stepwise addition; no more than 100 trees of score (length) greater than or equal to 602 saved in each replicate; number of rearrangements (per addition-sequence replicate) limited to 1,000,000,000.

Because of the large size of the matrix and limited processing power, it was necessary to restrict the analysis in order to complete it. For example, we attempted to run an analysis of 10 unrestricted random addition replicates. After 240 hours (10 days), the search had not proceeded past the first random addition replicate. The search tried $>2.04 \times 10^9$ rearrangements and had saved 180,550 equally parsimonious trees of 598 steps (of which it still had 179,005 remaining to be swapped). We chose to run an analysis in which multi-state characters for any taxon were interpreted as uncertain. This allowed PAUP to select the variable state that minimized tree length. A heuristic search consisting of 1000 random addition sequences was performed. In order to increase the chance of improving the tree score found by stepwise addition, 10 trees were held at each step. Only 1000 trees were held for each step greater than 602 steps. This value was determined by conducting numerous single random addition sequence searches. In all of these searches, trees of at least 602 steps were generated. Therefore, 602 was set as an upper limit to restrict searching of sub-optimal trees, which resulted in decreasing the overall time required to complete all 1000 replicates. In addition, the maximum number of branch swapping rearrangements was limited to 100,000,000 per repetition.

We recognize the inherent problems of placing too great a reliability on parsimony analyses of large data matrices, especially when there are relatively few characters per taxon and considerable homoplasy. We believe it worthwhile, however, to have the results of an analysis that is restricted essentially to characters derived from a single character-rich complex, dorsal gill-arch muscles and skeleton, that has received rel-

atively limited attention in the past (Johnson 1993: 27). In spite of the large amount of homoplasy involved, our analysis clearly represents stronger tests of the monophyly of the Smegmamorpha than Johnson and Patterson's (1993; henceforth, J&P) hypothesis based essentially on a single character (included in our analysis), mode of articulation of the anterior-most epineural. It may not be, however, an adequate test of Stiassny and Jensen's (1987) hypothesized monophyly of the Labroidei also based essentially on gill-arch skeletal and muscle characters (included in our analysis, but comprising only a few of the characters we address). Additionally, there is heuristic value in the clades we have found, which will provide bases for others to test or derive support.

Characters (Numbers in Brackets) and Character States (Numbers in Parentheses)

- [1] LE1 inserts completely medial to lateral fourth of surface of Eb1 (0); insertion includes all or part of lateral fourth of surface (1); LE1 absent (2).
- [2] LE1 origin groups with other LE origins (0); separate from other LE origins (1); not applicable (-).
- [3] LE3 present (0); vestigial or absent (1).
- [4] LP and LE4 insert together on Eb4 (0); insertions well separated on Eb4 (1); LE4 and/or LP sheet-like, usually continuous with PP, with broad attachment continuing from Eb4 and Cb5 along length of Cb4 (2); LP absent (3); LE4 absent.
- [5] LP does not insert by long, slender tendon (0); inserts by long, slender tendon (1); not applicable (-).
- [6] LI1 only on Pb2 (0); on Pb2 and Pb3 (1); only on Pb3 (2); on Pb2 and IAC (3); not applicable (-).
- [7] LI1 slightly, if at all, larger than LI2 (0); much larger than LI2 (1).
- [8] LI2 does not penetrate OD (0); penetrates OD (1).
- [9] TD muscles essentially completely cover Pb3s dorsally (0); TD muscle broadly replaced or interrupted medially by CT dorsal to Pb3s, Pb3s usually with flat, dorsal articulating facets, which do not form diarthrosis with process on ventral surface of cranium (1); TD muscles broadly replaced medially by CT dorsal to moderate-sized Pb3 dorsal articulating facets, facets join diarthrosis with irregular-surfaced knob-like process on ventral surface of cranium (2); TD muscle broadly replaced medially by CT dorsal to relatively large Pb3 dorsal articulating facets, facets form diarthrosis with smooth, con-

- forming, usually weakly bilobed ventral surface of process on ventral surface of cranium (3).
- [10] TEb2 right and left sides do not overlap medially (0); overlap medially (1); TEb2 absent (2).
- [11] TEb2 extends laterally well past medial edge of LE2 insertion (0); does not extend laterally much, if any, past medial edge of LE2 insertion (1); inapplicable (–).
- [12] TPb2 insertion not on IAC (0); insertion includes IAC (1); TPb2 vestigial or absent (2).
- [13] TPb2a absent (0); present (1).
- [14] TD attachments include Eb3 (0); exclude Eb3 (1).
- [15] TD not on Eb4 (0); on Eb4 (1).
- [16] TDP attaches to Pb3 (0); does not attach to Pb3 (1).
- [17] TD not attached to Pb4 when Pb4 is present (0); attached to Pb4 (1); Pb4 absent (2).
- [18] SOD present (0); absent (1).
- [19] CPb absent (0); present (1).
- [20] OD origin only on Pb3 (0); on Pb2 and Pb3 (1).
- [21] OD3' absent (0); present (1).
- [22] OD insertion includes Eb3 (0); excludes Eb3 (1).
- [23] OD on Eb4 (0); not on Eb4 (1).
- [24] OD4' absent (0); present (1).
- [25] OP posteroventrally mostly to entirely on Cb5 (0); wholly or partly on Cb4 and/or joining ER at level of Cb4 (1); OP absent (2).
- [26] Neither OP nor Ad4 joins either LE4 or LP when both LE4 and LP are present (0); OP joins only LE4, which is not released from Eb4; Ad4 not involved (1); OP joins only LE4, which is mostly released from Eb4; Ad4 not involved (2); OP joins only LP; Ad4 not involved (3); OP joins both LP and LE4, which is not released from Eb4; Ad4 not involved (4); OP joins both LP and LE4, which is released from Eb4; Ad4 not involved (5); Ad4 joins only LE4; OP not involved (6); Ad4 joins only LP; OP not involved (7); Ad4 joins both LP and LE4; OP not involved (8); Inapplicable (–).
- [27] M. Pb2-Eb2 absent (0); present (1).
- [28] M. Pb3p absent (0); present (1).
- [29] GFM1 moderately developed or absent, not fan-like (0); enlarged, fan-like (1).
- [30] Ad1 absent (0); present (1).
- [31] Ad2 and Ad3 absent (0); present (1).
- [32] Ad5 dorsally or anteriorly; attaches only to distal end of Cb4 and/or AC4 (0); attaches well medial to distal end of Cb4 and/or to ER well medial to distal end of Cb4 (1); attaches only or more than incidentally to Eb4 (2); Ad5 absent (3).
- [33] ER absent (0); present (1).
- [34] Ad5 joins neither LP nor LE4 (0); joins LE4 and/or LP (1); inapplicable (–).
- [35] TV4 free from Cb5s (0); attached to Cb5s (1); TV4 absent (2).
- [36] PCI attachment on Cb5 begins well medial to distal end and extends medially (0); attachment on Cb5 begins at distal end and extends medially, muscle does not join raphe with OP ventrally (1); attachment on Cb5 begins at distal end and extends medially, muscle joins raphe with OP ventrally (2).
- [36a] M. Pb3-Cb5 absent (0); present (1).
- [37] Pb1 bony and cartilaginous, articulates with anterior Eb1 process (0); Pb1 all cartilaginous, articulates with anterior Eb1 process (1); Pb1 absent, anterior Eb1 process present (2); Pb1 absent, Eb1 anterior process absent (3).
- [38] Pb2 with teeth (0); Pb2 edentate (1); Pb2 absent (2).
- [39] UP4 present (0); absent (1).
- [40] Cartilage-tipped Eb1 uncinatate process present (0); absent (1).
- [41] Cartilage-tipped Eb3 uncinatate process present (0); absent (1).
- [42] Eb4 bony flange absent (0); present (1).
- [43] Medial end of Eb4 equal to or smaller than medial end of Eb3 (0); larger than medial end of Eb3 (1). Character not discussed by S&J; observations coded directly in matrix.
- [44] Cartilage-tipped Eb4 uncinatate process present (0); absent (1).
- [45] Levator process present on Eb4 (0); absent (1).
- [46] AC1 absent (0); present (1).
- [47] AC2 absent (0); present (1).
- [48] AC3 absent (0); present (1).
- [49] AC4 present (0); absent (1).
- [50] IAC (or IAB) present (0); IAC absent (1).
- [51] Cb5s not fused together (0); fused but suture present (1); fused but suture absent (2).
- [52] SCL present (0); absent (1).
- [53] Anteriormost epineural rib does not articulate with distal end of transverse process (0); articulates with distal end of transverse process (1).
- [54] Eb1 not modified as suprabranchial organ (0); modified as suprabranchial organ (1).
- [55] Parasphenoid teeth absent (0); present (1).

Results

The results are summarized in two cladograms, one, a strict consensus tree (SCT; Figure 5) derived from the 1823 most parsimonious (retained) trees, each with 595 steps, found during the PAUP analysis, and the other, a 50 percent majority-rule tree (MRT; Figure 6). In the SCT, there are 77 non-terminal nodes (those present in all 1823 trees retained) and in the MRT there are 145 non-terminal nodes.

The large number of taxa surveyed made it impractical to show character and nodal support directly

Table 12.—Character-state matrix for selected acanthomorph taxa examined for present study. Family name followed by genus indicates characters coded only for genus; otherwise coding refers to all taxa examined. Characters 1–52 are those examined during present study. Assignment of states for character 53 are inferred from Johnson and Patterson (1993:table 2, character 3); 54 is based on Nelson (1994: 432, compiled); and 55 is based on R. Britz (pers. comm.) and literature. Other character states are assigned based on *Synagrops* (Acropomatidae), as a single outgroup. Key: A = (01); B = (02); C = (03); D = (06); E = (12); – = (not applicable); ? = (missing).

TAXA	Characters																			
	000	000	000	111	111	111	122	222	222	223	333	333	333	344	444	444	445	555	55	
	123	456	789	012	345	678	901	234	567	890	123	456	678	901	234	567	890	123	45	
	...	...	...	...	...	...	...	...	...	...	...	...	a...	...	...	...	...	...	...	
Acropomatidae	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	00	
Percichthyidae	000	000	000	000	000	000	000	000	010	000	000	000	000	000	000	000	000	000	00	
Pempheridae	000	000	000	001	000	000	000	000	000	000	000	000	000	000	000	000	A00	000	00	
Glaucosomatidae	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	100	000	00	
Ammodytidae	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	100	000	00	
Terapontidae, <i>Terapon</i>	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	00	
Terapontidae, <i>Leiopotherapon</i>	000	000	000	000	000	000	001	000	080	000	000	000	000	000	000	000	000	000	00	
Girellidae	000	100	000	000	00A	010	000	000	000	000	000	000	000	000	000	010	000	010	00	
Kuhliidae	000	003	000	001	000	010	000	000	000	000	000	000	000	000	000	010	000	000	00	
Epigonidae	000	000	000	001	000	000	00A	000	000	000	000	000	000	000	000	000	000	000	00	
Lactariidae	000	000	100	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	00	
Bathyclupeidae	000	003	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	00	
Ostracoberycidae	000	000	000	000	000	000	000	000	060	000	000	000	000	000	000	000	100	010	00	
Sebastidae	000	000	000	010	001	000	000	000	000	000	000	000	000	000	000	000	000	000	00	
Scorpaenidae	000	00A	000	010	001	000	000	000	000	000	000	000	000	000	000	000	000	010	00	
Platycephalidae, <i>Platycephalus</i>	000	001	000	002	011	000	010	000	000	000	010	000	000	000	000	000	000	010	00	
Lutjanidae	000	000	000	001	000	AA0	000	000	000	000	000	000	000	000	000	000	000	010	00	
Centrarchidae, <i>Micropterus</i>	000	000	000	000	000	010	000	000	000	000	000	000	000	000	000	000	000	010	00	
Moronidae	000	000	000	001	000	010	000	000	001	000	000	000	000	000	000	000	00A	000	00	
Latidae	000	000	100	000	000	000	000	000	060	000	000	000	000	000	000	000	000	000	00	
Centropomidae	000	000	100	000	010	000	000	000	060	010	000	000	000	000	000	000	1A0	A00	00	
Caristiidae	000	000	000	000	000	000	000	000	080	000	000	000	000	000	000	000	100	011	00	
Apogonidae, <i>Glossamia</i>	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	100	A00	010	00	
Kurtidae	000	001	000	000	000	120	000	000	000	000	000	000	000	000	000	000	100	010	00	
Cirrhitidae, <i>Paracirrhites</i>	000	000	000	000	010	000	000	000	000	000	000	002	000	000	010	000	010	000	00	
Percidae, <i>Perca</i>	000	001	000	000	000	010	010	000	000	000	000	000	000	000	000	010	100	010	00	
Percidae, <i>Percina</i>	000	001	000	000	000	010	010	000	001	001	100	000	030	000	010	100	01A	000	00	
Cepolidae, <i>Cepola</i>	000	001	000	002	000	000	000	000	000	000	000	000	000	000	000	000	000	000	00	
Serranidae	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	00	
Symphysanodontidae	000	000	000	01B	000	000	00A	000	000	000	000	000	000	000	000	000	A00	0A0	00	
Nematistiidae	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	100	000	00	
Malacanthidae	000	000	000	000	000	00A	100	000	000	000	000	000	000	000	000	000	000	010	00	
Carangidae, <i>Selar</i>	000	000	000	000	001	010	001	000	070	000	000	000	000	000	000	100	000	000	00	
Priacanthidae	000	000	000	002	011	001	000	000	000	000	000	000	000	000	000	000	000	0A0	00	
Centracanthidae	000	100	000	000	000	010	101	000	000	001	100	000	100	010	100	000	010	000	00	
Haemulidae	000	003	A00	002	000	011	001	000	070	000	000	000	000	000	000	100	000	000	00	
Inermiidae	000	000	000	002	000	011	001	000	070	000	000	000	000	000	000	100	000	000	00	
Nemipteridae	000	000	000	000	000	110	101	000	000	000	000	002	000	010	001	000	011	000	00	
Lateolabracidae	000	003	100	002	000	010	001	000	000	000	000	000	000	000	000	000	000	010	00	
Callanthiidae	000	000	000	002	0A0	010	00A	000	000	001	100	000	010	000	001	000	000	010	00	
Bramidae	001	003	000	000	011	000	000	000	000	000	000	000	000	000	000	000	000	010	00	
Icosteidae	000	001	000	010	001	100	000	000	100	000	011	000	000	A00	000	1A0	0A0	000	00	
Centrolophidae	000	000	001	000	000	011	000	000	?00	000	000	000	000	000	000	000	000	010	00	
Amarsipidae	000	000	000	000	010	010	001	000	000	000	000	000	000	000	000	100	010	000	00	
Mullidae	000	000	000	001	000	020	001	000	000	000	020	000	020	000	000	10A	010	010	00	
Sciaenidae, <i>Cynoscion</i>	000	003	100	002	000	000	000	000	000	000	000	002	000	000	000	100	000	010	00	
Rhacichthyidae	100	001	000	002	010	010	000	000	000	010	100	000	010	000	111	100	010	000	00	
Cichlidae, <i>Ptychochromis</i>	000	001	103	001	111	021	100	000	050	001	120	010	000	000	110	100	010	100	00	
Pomacentridae, <i>Dischistodus</i>	000	001	102	000	110	021	101	000	010	001	100	010	000	000	100	100	010	200	00	
Pomacentridae, <i>Amphiprion</i>	000	001	102	000	110	021	101	000	040	001	100	010	000	000	100	0AA	010	200	00	
Labridae, <i>Achoerodus</i>	000	002	003	2-0	111	021	100	000	050	001	120	010	011	101	110	111	111	200	00	
Labridae, <i>Choerodon</i>	000	002	003	2-0	111	021	100	000	050	001	120	010	011	101	110	10A	011	200	00	
Labridae, <i>Coris</i>	000	002	003	010	111	021	100	000	050	001	120	010	011	101	110	111	111	200	00	
Embiotocidae, <i>Amphistichus</i>	000	001	003	002	011	020	000	000	050	001	120	010	001	000	100	100	0A1	200	00	

Table 12.—Continued.

TAXA	Characters																			
	000	000	000	111	111	111	122	222	222	223	333	333	333	344	444	444	445	555	55	
	123	456	789	012	345	678	901	234	567	890	123	456	678	901	234	567	890	123	45	
	...	...	...	...	...	...	...	...	...	...	...	...	a..	...	...	...	...	...	...	
Embiotocidae, <i>Embiotoca</i>	000	000	003	002	011	021	000	000	050	001	120	010	001	000	100	000	001	200	00	
Pholidichthyidae	000	402	101	010	111	021	100	000	0-0	001	100	010	001	100	111	100	011	200	00	
Lethrinidae	000	110	000	000	0AA	0A0	101	000	000	001	100	00B	000	000	A01	000	010	010	00	
Sparidae	000	000	000	000	000	010	A01	000	000	001	100	000	100	000	100	000	010	000	00	
Draconettidae	000	002	000	002	000	120	100	000	000	001	120	000	010	110	001	100	011	000	00	
Champsodontidae	000	002	010	002	011	101	000	000	000	000	000	000	020	000	000	100	010	000	00	
Uranoscopidae, <i>Xenocephalus</i>	001	001	000	012	000	020	000	000	000	000	000	000	011	000	000	000	011	010	00	
Bovichtidae	000	001	000	002	010	010	001	000	000	001	100	000	030	000	000	100	011	000	00	
Pseudaphritidae	000	000	000	002	010	110	000	000	000	000	000	000	030	000	000	100	011	000	00	
Cheimarrichthyidae	000	001	000	002	000	000	000	000	000	000	000	000	010	000	000	100	010	000	00	
Trachinidae	000	001	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	000	00	
Plesiopidae, <i>Assessor</i>	000	001	10A	010	000	020	000	000	000	000	000	000	000	000	100	A00	010	000	00	
Grammatidae	000	001	101	002	010	010	000	000	000	000	000	010	000	000	100	000	010	000	00	
Opistognathidae, <i>Lonchopisthus</i>	000	001	001	002	001	000	000	000	000	000	000	010	001	000	10A	000	010	000	00	
Pseudochromidae	000	001	101	002	10A	000	000	000	000	001	120	010	0E0	000	100	000	01A	000	00	
Centrogeniidae	000	001	001	000	010	000	000	000	010	000	000	012	001	000	001	000	000	000	00	
Ambassidae, <i>Ambassis</i>	000	001	001	001	000	021	000	000	000	000	000	000	000	000	000	100	0A0	000	00	
Ambassidae, <i>Tetracentrum</i>	000	001	001	001	000	011	000	000	010	000	000	000	000	000	100	100	A10	000	00	
Bathymasteridae	000	001	100	000	000	020	000	000	000	000	000	000	030	000	000	100	011	000	00	
Anoplopomatidae	000	001	100	000	000	000	000	000	000	001	100	000	030	000	000	100	011	000	00	
Stichaeidae	000	001	100	002	000	000	001	000	000	001	100	000	030	000	000	100	011	000	00	
Hexagrammidae	000	001	000	000	000	000	000	000	000	000	000	000	010	000	000	100	010	000	00	
Gerreidae	000	001	001	002	001	000	00A	000	000	001	100	000	000	000	1A0	100	010	000	00	
Polynemidae	000	00A	000	010	000	010	000	000	000	000	000	000	000	000	010	100	010	010	00	
Toxotidae	000	000	001	001	000	010	000	000	010	000	000	000	000	000	100	000	010	000	00	
Polycentridae, <i>Afronandus</i>	001	001	100	002	001	021	000	000	000	000	000	000	000	000	000	100	010	000	00	
Polycentridae, <i>Monocirrhus</i>	001	001	100	002	001	021	001	000	000	000	010	000	000	000	0A0	100	010	000	00	
Polycentridae, <i>Polycentropsis</i>	001	001	000	002	001	021	000	000	000	000	000	000	000	000	000	100	010	000	00	
Polycentridae, <i>Polycentrus</i>	001	001	100	000	001	021	000	000	000	000	000	000	000	000	000	000	010	000	00	
Nandidae	001	000	000	002	001	021	000	000	000	000	001	100	000	000	010	100	000	010	000	
Badidae	001	000	001	002	011	021	000	000	070	001	100	000	010	010	100	A00	010	000	01	
Pristolepidae	000	000	001	002	011	121	000	000	000	000	020	001	000	010	010	000	010	000	01	
Channidae	000	002	000	012	011	021	100	000	030	000	1B0	001	000	010	111	100	011	000	11	
Anabantidae, <i>Sandelia</i>	000	002	001	2-0	010	021	100	000	000	000	020	001	000	0A0	111	100	01A	000	11	
Caproidae, <i>Antigonia</i>	000	010	000	002	001	020	001	010	000	000	000	000	000	000	000	100	01A	000	00	
Caproidae, <i>Capros</i>	100	3-0	000	012	001	120	001	010	060	001	100	000	000	000	000	100	011	000	00	
Sillaginidae	000	003	000	000	000	000	001	000	001	000	100	000	000	000	100	101	010	000	00	
Dactylopteridae	000	002	100	000	000	020	000	000	000	001	100	000	010	000	000	100	011	000	00	
Mugilidae, <i>Agonostomus</i>	010	000	000	011	010	02A	000	000	000	000	120	000	000	000	100	100	010	001	00	
Bedotiidae	010	100	001	2-0	111	021	000	000	020	000	120	000	000	000	110	100	010	001	00	
Atherinidae	010	100	001	2-0	111	021	000	100	030	001	120	000	000	000	110	100	010	001	00	
Adrianichthyidae, <i>Xenopoecilus</i>	111	100	001	2-0	110	021	000	100	000	000	120	000	020	110	111	100	010	001	00	
Cyprinodontidae	111	102	001	2-0	111	021	000	100	000	001	100	020	020	110	110	100	010	001	00	
Aplocheilidae	110	000	001	2-0	110	021	000	100	000	001	120	010	020	010	110	100	010	001	00	
Hemiramphidae	010	100	001	2-0	111	021	000	100	020	100	100	010	020	100	110	1A1	010	201	00	
Exocoetidae	110	000	001	2-0	111	021	000	100	020	100	100	010	020	110	110	1A0	010	201	00	
Belonidae, <i>Strongylura</i>	110	000	001	2-0	?11	020	000	000	001	000	13-	010	020	111	111	110	A?1	201	00	
Belonidae, <i>Tylosurus</i>	111	000	000	2-0	?11	020	000	100	001	000	13-	010	020	111	111	1A0	0?1	201	00	
Scomberesocidae	011	000	001	2-0	110	020	000	100	0C1	000	100	010	020	100	011	1A0	011	201	00	
Elassomatidae	100	001	100	002	001	020	000	000	000	001	100	000	030	000	001	100	011	001	00	
Gasterosteidae, <i>Apeltes</i>	001	001	000	012	001	020	000	000	000	001	120	100	030	100	010	100	011	001	00	
Gasterosteidae, <i>Culea</i>	001	001	100	012	001	020	000	000	000	001	120	100	030	100	000	100	011	001	00	
Gasterosteidae, <i>Gasterosteus</i>	001	001	100	012	001	020	000	000	000	001	120	100	030	100	000	100	011	001	00	
Gasterosteidae, <i>Pungitius</i>	001	001	100	012	001	020	000	000	000	001	120	100	030	100	010	100	011	001	00	
Gasterosteidae, <i>Spinachia</i>	001	001	100	012	001	020	000	000	000	001	120	100	030	100	010	100	011	001	00	
Aulorhynchidae	101	001	100	012	001	020	001	000	070	001	100	000	030	000	000	100	011	001	00	
Hypoptychidae, <i>Aulichthys</i>	100	001	000	012	010	020	010	000	000	001	100	000	030	100	000	100	011	001	00	
Hypoptychidae, <i>Hypoptychus</i>	100	3-0	000	002	010	000	010	000	060	001	120	100	030	100	000	100	011	001	00	

Table 12.—Continued.

TAXA	Characters																			
	000	000	000	111	111	111	122	222	222	223	333	333	333	344	444	444	445	555	55	
	123	456	789	012	345	678	901	234	567	890	123	456	678	901	234	567	890	123	45	
	...	...	...	...	...	...	...	...	...	...	...	...	a...	...	...	...	...	...	...	
Synbranchidae	101	3--	100	012	001	020	000	000	0-0	001	100	000	021	010	111	100	010	011	00	
Mastacembelidae	001	3-1	100	012	000	000	000	000	0-0	001	100	002	030	010	010	100	011	011	00	
Centriscidae	001	000	000	002	000	020	011	000	100	010	021	000	010	010	000	100	011	001	00	
Leptobramidae	000	000	000	001	001	000	001	000	000	000	000	001	000	000	000	000	000	000	00	
Tripterygiidae, <i>Ruanoho</i>	100	002	000	012	010	021	000	000	000	001	100	011	022	111	001	100	011	000	00	
Tripterygiidae, <i>Lepidoblennius</i>	100	002	001	012	010	021	000	000	030	001	100	112	022	111	011	100	011	000	00	
Dactyloscopidae	001	002	001	0A2	011	020	000	000	000	000	000	011	022	111	011	100	011	000	00	
Chaenopsidae	000	002	001	002	011	020	000	000	000	000	000	012	012	111	001	100	011	000	00	
Labrisomidae, <i>Calliclinus</i>	000	002	001	000	011	021	000	000	010	000	020	012	012	111	001	100	011	000	00	
Clinidae, Clininae	A00	002	001	002	011	020	000	000	040	000	000	012	0E2	111	0A1	100	011	000	00	
Clinidae, Myxodinae	100	002	001	002	011	020	000	000	0A0	000	020	012	012	111	011	100	011	000	00	
Blenniidae	100	002	00A	002	01A	020	000	A00	000	001	100	012	022	111	011	100	011	000	00	
Berycidae	000	010	000	010	00A	020	000	000	100	000	001	000	000	000	010	100	001	010	00	
Trachichthyidae	000	3-0	000	010	000	020	000	000	1-0	000	001	000	000	100	010	100	011	010	00	
Grammicolepidae	100	011	100	000	000	121	001	010	100	000	010	000	000	110	010	000	011	010	00	
Oreosomatidae	101	001	000	010	000	121	001	010	100	000	011	000	000	110	010	100	011	000	00	
Triacanthodidae	000	010	002	000	000	020	000	010	000	010	000	000	000	000	000	100	010	000	00	
Menidae	000	200	000	012	000	021	001	010	100	000	001	000	000	000	000	100	100	000	00	
Leiognathidae	100	0-0	001	002	00A	100	001	010	050	000	000	010	000	010	100	100	011	000	00	
Ephippidae, <i>Chaetodipterus</i>	100	010	000	002	001	100	001	010	060	000	000	000	000	0A0	100	100	00A	000	00	
Luvuridae	000	200	000	002	011	000	000	010	010	000	000	000	000	000	000	100	010	000	00	
Zanclidae	100	200	100	002	001	100	010	010	000	000	000	000	000	000	001	100	011	000	00	
Acanthuridae	100	2?0	000	002	011	100	000	010	0?0	010	000	000	000	010	000	100	001	000	00	
Holocentridae	000	000	100	000	011	000	000	000	100	000	011	000	000	000	010	100	011	010	00	
Aphredoderidae	001	000	000	2-0	011	101	010	001	001	000	000	000	000	000	010	000	011	010	00	
Percopsidae	001	000	000	2-0	011	000	010	101	001	000	000	000	000	000	010	000	011	010	00	
Amblyopsidae	101	000	000	2-0	011	100	010	101	001	000	000	000	030	000	010	000	011	010	00	
Stephanoberycidae	000	000	000	010	010	000	001	000	160	000	011	000	001	101	001	100	011	000	00	
Gibberichthyidae	000	000	000	2-0	010	000	000	000	160	000	011	000	001	000	0A0	100	011	000	00	
Rondeletiidae	000	000	000	2-0	010	000	000	000	100	000	011	000	001	000	000	100	011	000	00	
Cetomimidae	2-1	000	000	010	001	100	000	000	000	000	030	-00	001	001	011	100	011	010	00	
Barbouriidae	000	000	000	010	010	000	000	000	110	000	011	000	000	000	010	100	011	000	00	
Melamphaidae	000	000	000	010	000	021	000	000	100	000	001	000	000	000	010	100	011	010	00	
Lampridae	000	2-0	000	102	001	100	011	000	?00	000	00?	000	000	010	001	00A	011	000	00	
Veliferidae, <i>Velifer</i>	000	3-0	000	102	001	010	000	000	0-0	000	000	000	000	000	011	000	101	000	00	
Polymixiidae	000	010	100	010	000	000	000	000	100	000	011	000	000	000	000	000	011	000	00	
Gobiesocidae	001	002	000	012	011	020	000	000	000	001	120	001	022	111	001	100	011	010	00	
Rhamphocottidae	001	001	000	000	000	020	001	000	000	000	010	000	000	100	000	100	011	000	00	
Ranicipitidae	001	002	100	002	001	020	000	000	100	000	011	000	010	100	010	100	011	010	00	
Batrachoididae	001	3-1	000	002	001	121	000	000	0-0	000	010	000	000	100	000	100	010	000	00	
Ophidiidae, <i>Brotula</i>	000	3-0	110	010	000	100	001	000	161	000	011	000	000	010	000	100	011	010	00	
Ophidiidae, <i>Dicrolene</i>	000	3-0	000	2-0	000	0A0	000	000	1-1	000	011	000	000	000	000	100	010	010	00	
Bythitidae, <i>Calamopteryx</i>	000	3-0	110	2-0	000	020	000	000	1-1	000	011	000	030	000	000	100	011	010	00	
Chaunacidae	001	3-2	000	010	011	120	000	000	-D1	000	030	-00	000	100	000	100	011	010	00	
Scombridae, <i>Scomber</i>	000	3-0	000	010	000	020	001	000	0-0	000	000	000	000	000	010	100	000	000	00	
Sphyracidae	000	000	100	010	000	020	000	000	000	000	000	000	000	000	010	100	010	010	00	
Pomatomidae	000	000	000	011	000	000	001	000	010	000	000	000	000	000	000	000	010	000	00	
Scombrobracidae	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	000	010	010	00	
Rachycentridae	000	100	100	002	000	010	001	000	000	000	000	000	000	000	000	000	000	000	00	
Coryphaenidae	000	100	000	000	000	100	001	000	000	000	000	001	000	000	000	100	000	010	00	
Zaproridae	000	001	100	000	000	000	000	010	000	000	000	000	030	000	000	100	011	000	00	
Psettodidae	001	000	000	010	011	120	000	000	000	000	000	000	000	000	000	100	010	000	00	
Zeniontidae	001	??1	100	000	000	121	001	000	??0	000	00?	000	000	110	010	100	011	000	00	
Parazenidae	001	002	100	2-0	000	021	001	000	000	000	000	000	000	110	010	100	011	000	00	
Anomalopidae, <i>Anomalops</i>	000	000	100	010	000	020	000	000	160	000	001	000	000	100	010	100	010	000	00	
Anomalopidae, <i>Photoblepharon</i>	000	000	000	010	001	020	000	000	160	000	001	000	000	100	010	100	010	000	00	

on the subsequent phylogenetic trees. We chose to represent these values for the MRT in Table 13, rather than to enlarge the tree and split it across multiple pages. In the MRT (Fig. 6) we designated four major clades with letters (A, B, C, D) and then labeled all internal nodes with numbers in boxes (starting from the top left hand side of the tree and sequentially working towards the terminal nodes whenever possible). In Table 13, we chose only to show those characters that support a node unambiguously and included both uncontradicted synapomorphic and homoplastic characters. We have given the character state for each supporting character, but have not shown a direction of change, as all data were run unordered.

The cladograms include a mix of interrelationships that have been suggested or formally hypothesized by other workers (usually based on few, if any, of the characters used in our analysis) and some that have never been proposed. Among the latter are many we suspect are unreasonable, but some of these probably deserve serious consideration. We believe that the SCT obscures much of the phylogenetic signal; therefore, the following discussion is based mainly on the MRT. We restrict most of our discussion to those clades we believe are most informative or corroborated by other studies. The interrelationships implied by the PAUP analysis had no influence on S&J's suggested interrelationships.

Bolded letters in brackets [] refer to the four major nodes in the MRC (Fig. 6); numbers following the bolded letters refer to small boxed numbers of non-terminal nodes included in the major node, e.g., [A 13].

LAMPRIDIFORMES (Veliferidae, Lampridae), ACANTHUROIDEI, CAPROIDAE, LEIOGNATHIDAE [B 40]. The MRC retrieved the two families of lampridiforms as a sister group [B 41], which is sister to a clade [B 42] comprising all the acanthuroids (except Luvaridae) we examined, Leiognathidae, and *Capros*, one of the two genera of Caproidae. Luvaridae are included in a larger clade [B 32] containing the taxa mentioned, but they are well removed stepwise from them. Both Tyler et al. (1989) and Winterbottom (1993a), hypothesized Luvaridae as a member of the Acanthuroidei in well-defended phylogenetic analyses, and we believe their affinities are with the acanthuroids. The other genus of caproid, *Antigonia*, was retrieved as sister group to the Triacanthodidae (*Parahollardia*) in a clade [D 120] well removed from that containing *Capros*.

S&J discussed Tyler et al.'s (2003) study in which the latter's preferred cladistic analysis retrieved both caproid genera, the tetraodontiform genus *Parahollardia* and their other outgroups in a polytomy with the zeiforms. If acanthuroids, among which *Capros* was retrieved in our analysis, and tetraodontiforms,

with which *Antigonia* was retrieved, are perciforms, J&P's claim that caproids are perciforms (or at least percomorphs) is corroborated, although caproid monophyly remains problematic.

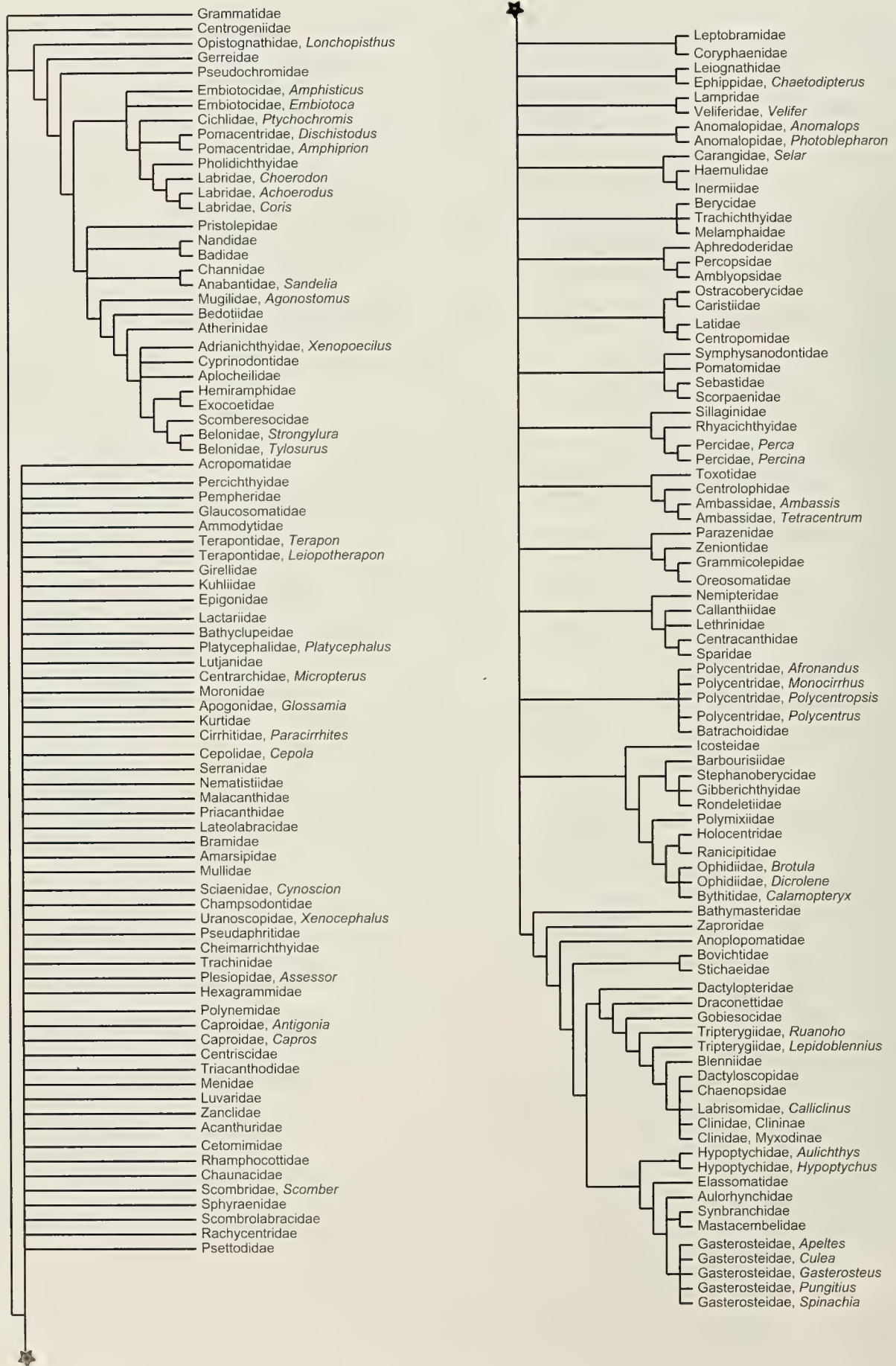
A caproid-tetraodontiform relationship has also been found in two recent molecular studies, Chen et al. (2003) and Miya et al. (2003). Chen et al. (2003), who included only *Capros*, presented the results of three different molecular analyses and a simultaneous analysis (their fig. 5) of the data on which the three separate analyses were based. The simultaneous analysis shows *Capros* as the sister group of the tetraodontiform *Mola*. One of the other three analyses has a clade with *Capros*, *Drepane* (an acanthuroid relative), and *Mola*. The other two analyses link *Capros* with a pleuronectiform or syngnathiform. Miya et al. (2003), who included only *Antigonia*, retrieved it as sister to the tetraodontiform genera *Stephanolepis* (Monacanthidae) and *Sufflamen* (Balistidae), a clade deeply nested among their percomorphs.

Considering all the studies together, the evidence hints at the possibility that there is a monophyletic group comprising caproids, acanthuroids, and tetraodontiforms. A close relationship between the last two groups was discussed and rejected by Rosen (1984), but we strongly believe deserves further study.

The interrelationships of the Leiognathidae have never been seriously investigated. They have been placed near the Menidae in classifications beginning with Bleeker (1859:xxiii), who included them with the fossil genus *Acanthonemus* Agassiz, an acanthuroid, (J.C. Tyler, pers. comm.), as the only members of his family Equulidae (= Leiognathidae, see discussion of proper family name in S&J). S&J hypothesized that the Menidae, which along with the Leiognathidae, have long been considered to be perciforms, are probably a pre-percomorph group, and our cladistic analysis corroborates that by retrieving Menidae well nested in a clade [D 130] containing beryciforms and stephanoberyciforms. We believe, however, that there is a good possibility that the leiognathids' closest relationships, as evidenced by our analysis, are with the acanthuroids.

POLYMIXIIFORMES. The MRT retrieved the Polymixiidae as part of a clade [D 137] that also includes a beryciform (*Holocentrus*) and two of the Paracanthopterygian groups, a gadiform (*Raniceps*) and the ophidiiforms. The sister group of this clade [D 134] contains all but one of the stephanoberyciforms, Cetomimidae [B 36], included in our study.

J&P (1993:fig. 24) hypothesized (Lampridiformes (Polymixiidae (Paracanthopterygii))) as the three basalmost groups of the Acanthomorpha. Wiley et al., (2000:fig. 6), in a combined molecular-morphological study, hypothesized the same two basalmost acanthomorph groups, but retrieved the Paracanthopterygii as polyphyletic: ((paracanthop percopsiforms (para-



canthop gadiforms + zeiforms) + (mix of groups, of which most deeply nested are some paracanthops)). Miya et al. (2003:fig. 2), in a molecular study, hypothesized a somewhat similar arrangement, with Polymixiidae as sister group of a group comprising percopsiforms, gadiforms and zeiforms. Chen et al. (2003, fig. 6C), in another molecular study, summarized their series of three molecular studies (see SMEGMAMORPHA, below) and included Polymixiiformes in the Paracanthopterygii.

The evidence presently is mixed as to whether Polymixiidae are the sister group of all other acanthopterygians (except lampridiforms) or should be included among a group comprising some of the paracanthopterygians (which could be the sister group of all other acanthomorphs).

PARACANTHOPTERYGII: PERCOPSIFORMES, LOPHIIFORMES (CHAUNACIDAE), OPHIDIIFORMES, GADIFORMES (RANICIPITIDAE), BATRACHODIFORMES (BATRACHODIDAE). The MRT retrieved the Paracanthopterygii as polyphyletic, its five components comprising parts of four separate monophyletic groups.

1) [B 37] Percopsiformes, Chaunacidae. The freshwater percopsiforms were retrieved as a resolved monophyletic clade [B 38] (Aphredoderidae (Percopsidae + Amblyopsidae)) that is the unlikely sister group of the moderately deep-dwelling, marine Chaunacidae. S&J hypothesized monophyly of percopsiforms based on eight characters (for discussion of the recent vacillating history of the group see S&J's account of Percopsiformes).

While the resolution of the Percopsiformes we report will probably undergo rearrangement, we feel confident that the monophyly of the three families will be further corroborated. Molecular studies (Wiley et al. 2000; Miya et al. 2003) have included only two percopsiforms, aphredoderids and percopsids, in their analyses and these indicate that the two families form a sister group; however, it is the phylogenetic position of Amblyopsidae that has been the source of most disagreement.

2) Ophidiiformes [D 140] are monophyletic, but Ophidiidae are paraphyletic without inclusion of Bythitidae. J. Nielsen (pers. comm.) informs us that there is increasing support for combining these two families.

3) [D 139] Ranicipitidae (sister group of all other gadiforms; Yabe 1985) seems unlikely to be closely related to the beryciform Holocentridae with which it is paired in [D 139], but close relationship of Ran-

icipitidae with Ophidiiformes, as indicated by node [D 137] is probable.

4) [C 63] Batrachoididae are well nested within the perciform family Polycentridae [C 60]. We believe a close relationship between these two groups to be improbable.

Markle (1989) hypothesized the batrachoidids as sister group of the gadiforms, of which Ranicipitidae are the basal member. Patterson and Rosen (1989) hypothesized batrachoidids and lophiiforms as sister group to the gadiforms, and Wiley et al. (2000:fig. 6), found batrachoidids to be the sister group of bythitids. Miya et al. (2003:fig. 2) found gadiforms to be the sister group of zeiforms. Thus, the interrelationships of all these groups remains problematic, but in all studies, except ours, the evidence indicates that batrachoidiforms are related to a pre-perciform group.

STEPHANOBERYCIFORMES. The MRT retrieved the five families in two separate and well removed clades. Four of the families were retrieved in a resolved clade [D 134], the fifth family, Cetomimidae, was retrieved as part of a clade [B 36] containing a variety of taxa. Paxton et al. (2001) suggested that Rondeletiidae and Gibberichthyidae are sister taxa, but the two are separated by Stephanoberycidae in the MRT.

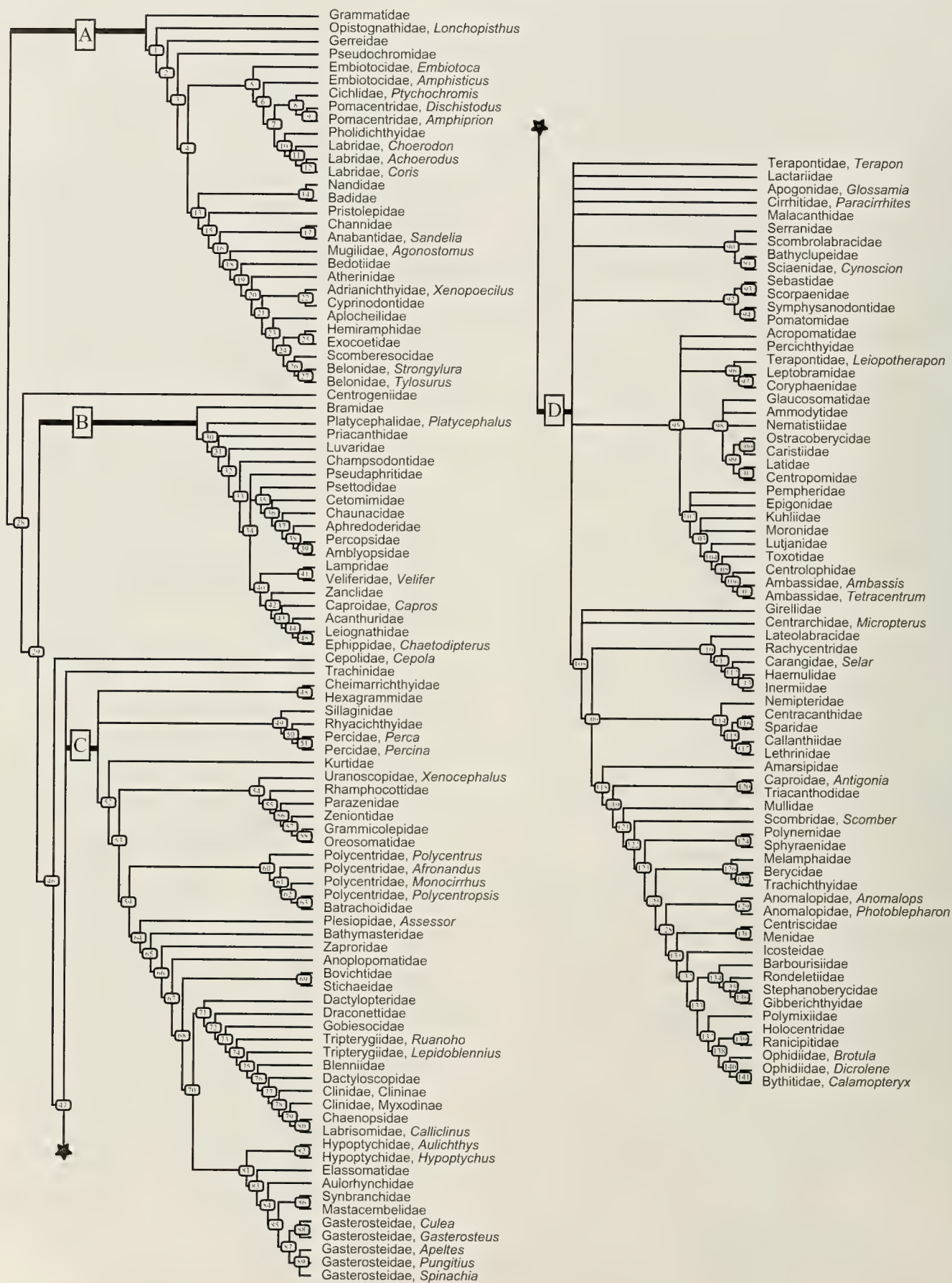
ZEIFORMES [C 56]. In the MRT, zeiforms comprise a monophyletic group that is the sister group of the Rhamphocottidae. We know of no other evidence for a zeiform-rhamphocottid relationship.

Although we examined few zeiform taxa, their stepwise arrangement in the MRT partly differs from their relative positions in the recent classification hypothesized by Tyler et al. (2003). Of the taxa in their classification, Oreosomatidae are the least specialized zeiform family that we examined. The MRT, however, retrieved Parazenidae and Zeniontidae as the first two branches of the clade. The position of Parazenidae and Zeniontidae in our analysis agrees with J&P's (1993:596) assertion that these families are the most plesiomorphic zeiforms. The MRT positions are also supported by Miya et al.'s (2003) molecular study based on complete mitochondrial DNA sequences, in which they reported essentially the same arrangement as in our MRT: (Parazenidae (Zeniontidae (Oreosomatidae + Zeidae))).

Holocentridae [D 139]. The position of the Holocentridae, whether its affiliations are with the beryciforms or the percomorphs, has been the subject

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Fig. 5. Strict consensus of 1,823 equally parsimonious trees (EPT) generated from a restricted parsimony analysis of 147 families of acanthomorph fishes (see Appendix for analysis specifics). Each EPT has 595 steps, consistency index 0.14, homoplasy index 0.86, and re-scaled consistency index 0.09. Star character indicates continuation of tree which is split into two columns. Tree is mid-point rooted.



of much current debate. Baldwin and Johnson (1995) discussed the evidence, which they found inconclusive. The MRT retrieved the Holocentridae as sister group of the gadiform Ranicipitidae among a larger group of clades [D 133] comprising ophidiiforms, stephanoberyciforms, and *Polymixia*. Holocentrids possess ER, which is restricted to pre-perciforms, and the putative percomorph families Centriscidae, Menidae, and Icosteidae, which we believe are pre-perciforms and which our MRT also retrieved among a clade [D 123] that includes many of those fishes.

SMEGMAMORPHA. The MRT retrieved the taxa J&P (1993) included in the Smegmamorpha (Synbranchiformes, Ellassomatidae, Gasterosteiformes, Mugilidae, Atherinomorpha) as a polyphyletic assemblage of three clades, none of which appears as closely related to another: Clade [A 18], Mugilidae + Atherinomorpha; Clade [C 81], Gasterosteiformes (less Centriscidae), Ellassomatidae, and Synbranchiformes; Clade [D 130], Centriscidae (+ Menidae). Clearly, J&P's putative smegmamorph synapomorphy (character 53) was swamped by other characters.

Clade [A 18] appears as the final branch in a clade [A 13] that includes the Anabantomorpha as its basal members. Clade [C 81] appears as the seemingly unlikely sister group of a clade [C 70] comprising the Dactylopteridae, Gobiesociformes (Draconettidae, Gobeisocidae), and Blennioidei. Clade [D 130] was retrieved as the sister group of Menidae among a clade [D 125] of pre-perciforms that also includes the Icosteidae.

The monophyly of the Smegmamorpha was first rejected by Nelson (1994:252–253), who placed Mugilomorpha at the base of the Acanthopterygii, followed by a branch, Atherinomorpha, which was separated by several branches from a polyphyletic Gasterosteiformes + Synbranchiformes. Wiley et al. (2000:figs. 6 and 8), in a combined morphological and molecular cladistic study, failed to retrieve a monophyletic Smegmamorpha. Neither Chen et al. (2003), in their three molecular analyses (see following), nor Miya et al. (2003), using mitogenomic data, recovered a monophyletic Smegmamorpha. Other than J&P's (1993) minimally supported hypothesis, no one has shown support for a monophyletic Smegmamorpha. Considering our results together with those of the other studies mentioned, there is no basis for recognizing the taxon. Older names are available for each of its originally hypothesized components and we suggest that Smegmamorpha be permanently

rejected for nomenclatural purposes. Discussion of its purported three clades follows.

Clade [A 18]. A sister-group relationship of the Mugilidae (= Mugilomorpha) and Atherinomorpha has been suggested by many authors over the years, but the most recent morphological studies (Stiassny 1993; Parenti, in press) consider the relationship problematic. Molecular studies are also problematic, but show a tendency of support of the relationship. Miya et al. (2003), in a mitogenomic study including 100 species representing all but one (Batrachoidiformes) of the higher teleostean orders, retrieved a clade (((Mugilidae) + (Blenniidae + Gobiesocidae)) + (Atherinomorpha)), which hints strongly at a mugilomorph-atherinomorph relationship. Chen et al. (2003), in a study of acanthomorphs, reported on three analyses: (1) 12S and 16S mtDNA from 97 taxa; (2) 28S rDNA from 74 taxa; (3) nuclear protein-coding gene, rhodopsin from 86 taxa. In (1), atherinomorphs were polyphyletic, but one of the clades with atherinomorphs has ((Mugilidae + Atherinomorpha) + (Blennioidei + Gobiesocidae)). In (2), atherinomorphs are also polyphyletic, but one clade has ((Mugilidae + Atherinidae) + (Serranidae)). In (3), atherinomorphs are monophyletic, and the clade is (Mugilidae + Atherinomorpha). In a combined analysis of the three analyses, atherinomorphs are polyphyletic, but the clade containing all atherinomorphs and the mugilid is ((Poeciliidae + Mugilidae) + (Bedotiidae + Belonidae)).

Including our study, there appears to be growing support for a monophyletic Mugilomorpha-Atherinomorpha sister group. To formally acknowledge this sister-group, and simplify future discussion of it, we resurrect Cope's (1871:480) *Percesoces*, in which he included only Mugilidae and Atherinidae, as its ordinal-group name.

The branchings of the Atherinomorpha in Clade [A 18] have been the subject of many studies since Rosen (1964) first proposed the group. Parenti (In press) presents a considered review of the relevant post-1964 literature and summarizes current hypotheses of atherinomorph inter- and intra-relationships. The intra-relationships of the atherinomorphs as retrieved by our MRT generally reflect those proposed in the literature, with the major difference being that the positions of Adrianichthyidae and Aplocheilidae in our tree are exchanged.

Clade [C 81] supports J&P's (1993:578–579) hypothesis that an Aulorhynchidae including *Aulorhynch*

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Fig. 6. 50% majority rule consensus of 1823 equally parsimonious trees (EPT) generated from a restricted parsimony analysis of 147 families of acanthomorph (see Appendix for analysis specifics). EPT statistics are as in Fig. 5. Four major clades are lettered A, B, C, and D. All other internal nodes are numbered in boxes. Character support for all nodes and frequency values for internal nodes are found in Table 13. Star character indicates continuation of tree, which is split into two columns. Tree is mid-pointed rooted.

Table 13.—Support values for all nodes of majority rule consensus tree (MRT; Fig. 6). Taxonomic names indicate terminal nodes. A, B, C, D refer to four major internal clades. Numbered nodes refer to clades within A, B, C, D. Bold and underlined characters are uncontradicted synapomorphies. All other characters are homoplastic. Character state follows colon and each character is separated by a comma. Frequency (*F*) corresponds to nodes represented in at least 50% of all 1823 equally parsimonious trees. Symbols: — = no support or support ambiguous; n/a = not applicable.

Node	Supporting Characters	<i>F</i>	Node	Supporting Characters	<i>F</i>
A	42:1	100	Cheimarrichthyidae	12:2	n/a
B	15:1	96	Cichlidae, <i>Ptychochromis</i>	12:1, <u>51:1</u>	n/a
C	45:1	96	Cirrhitidae, <i>Paracirrhites</i>	14:1, 36:2, 43:1	n/a
D	6:0	79	Clinidae, Clininae	26:4	n/a
Acanthuridae	14:1, 29:1	n/a	Clinidae, Myxodinae	—	n/a
Acropomatidae	—	n/a	Coryphaenidae	4:1, 16:1, 45:1, 52:1	n/a
Adrianichthyidae, <i>Xenopoecilus</i>	15:0, 44:1	n/a	Cyprinodontidae	6:2, 32:0, <u>35:2</u>	n/a
Amarsipidae	14:1	n/a	Dactylopteridae	12:0	n/a
Ambassidae, <i>Ambassis</i>	17:2	n/a	Dactyloscopidae	3:1, 36:1	n/a
Ambassidae, <i>Tetracentrum</i>	26:1, 42:1	n/a	Draconettidae	16:1, 19:1	n/a
Amblyopsidae	1:1, 37:3	n/a	Elassomatidae	44:1	n/a
Ammodytidae	—	n/a	Embiotocidae, <i>Amphisticus</i>	18:0	n/a
Anabantidae, <i>Sandelia</i>	10:2, 15:0, 31:0	n/a	Embiotocidae, <i>Embiotoca</i>	49:0	n/a
Anomalopidae, <i>Anomalops</i>	7:1	n/a	Ephippidae, <i>Chaetodipterus</i>	—	n/a
Anomalopidae, <i>Photoblepharon</i>	15:1	n/a	Epigonidae	—	n/a
Anoplopomatidae	—	n/a	Exocoetidae	—	n/a
Aphredoderidae	18:1	n/a	Gasterosteidae, <i>Apeltes</i>	7:0	n/a
Aplocheilidae	15:0	n/a	Gasterosteidae, <i>Culea</i>	—	n/a
Apogonidae, <i>Glossamia</i>	42:1	n/a	Gasterosteidae, <i>Gasterosteus</i>	—	n/a
Atherinidae	26:3	n/a	Gasterosteidae, <i>Pungitius</i>	—	n/a
Aulorhynchidae	21:1, 26:7	n/a	Gasterosteidae, <i>Spinachia</i>	—	n/a
Badidae	26:7, 37:1	n/a	Gerreidae	35:0, 45:1	n/a
Barbouriidae	26:1, 43:1	n/a	Gibberichthyidae	—	n/a
Bathylupeiidae	—	n/a	Girellidae	4:1, 43:1	n/a
Bathymasteridae	—	n/a	Glaucosomatidae	—	n/a
Batrachoididae	4:3, 16:1, 39:1	n/a	Gobiesocidae	3:1, 15:1, 52:1	n/a
Bedotiidae	26:2	n/a	Grammatidae	7:1, 17:1	n/a
Belonidae, <i>Strongylura</i>	22:0	n/a	Grammicolepidae	3:0, 5:1, 45:0, 52:1	n/a
Belonidae, <i>Tylosurus</i>	9:0	n/a	Haemulidae	6:3	n/a
Berycidae	49:0	n/a	Hemiramphidae	1:0, 4:1, 40:0, 47:1	n/a
Blenniidae	—	n/a	Hexagrammidae	—	n/a
Bovichtidae	7:0, 14:1, 17:1	n/a	Holocentridae	14:1	n/a
Bramidae	3:1, 6:3	n/a	Hypoptychidae, <i>Aulichthys</i>	11:1	n/a
Bythitidae, <i>Calamopteryx</i>	17:2, 37:3	n/a	Hypoptychidae, <i>Hypoptychus</i>	4:3, 6:0, 17:0, 26:6, 32:2, 34:1	n/a
Callanthiidae	12:2, 19:0, 37:1	n/a	Icosteidae	6:1, 15:1, 16:1	n/a
Caproidae, <i>Antigonia</i>	12:2, 15:1	n/a	Inermiidae	—	n/a
Caproidae, <i>Capros</i>	4:3, 11:1, 17:2, 30:1, 31:1	n/a	Kuhliidae	6:3, 43:1	n/a
Carangidae, <i>Selar</i>	12:0, 15:1	n/a	Kurtidae	16:1	n/a
Caristidae	26:8, 50:1	n/a	Labridae, <i>Achoerodus</i>	—	n/a
Centracanthidae	4:1, 40:1	n/a	Labridae, <i>Choerodon</i>	—	n/a
Centrarchidae, <i>Micropterus</i>	—	n/a	Labridae, <i>Coris</i>	—	n/a
Centriscidae	3:1, 11:0, 20:1, 29:1, 32:2, 37:1, 40:1, 50:1, 53:1	n/a	Labrisomidae, <i>Calliclinus</i>	12:0, 18:1, 26:1	n/a
Centrogeniidae	26:1, 36:2, 38:1, 44:1, 49:0	n/a	Lactariidae	7:1	n/a
Centrolophidae	12:0	n/a	Lampridae	20:1, 21:1, 40:1	n/a
Centropomidae	14:1, 29:1	n/a	Lateolabracidae	6:3	n/a
Cepolidae, <i>Cepola</i>	49:0	n/a	Latidae	45:0	n/a
Cetomimidae	<u>1:2</u> , 14:0, 38:1, 41:1, 44:1	n/a	Leiognathidae	9:1, 26:5, 35:1	n/a
Chaenopsidae	6:2, 8:1, 18:1, 37:2	n/a	Leptobramidae	12:1, 15:1	n/a
Champsodontidae	—	n/a	Lethrinidae	4:1, 5:1	n/a
Channidae	9:0, 26:3	n/a	Lutjanidae	—	n/a
Chaunacidae	4:3, 6:2, 17:2, 39:1	n/a	Luvaridae	4:2, 23:1, 26:1	n/a
			Malacanthidae	19:1	n/a

Table 13.—Continued.

Node	Supporting Characters	F	Node	Supporting Characters	F
Mastacembelidae	15:0, 17:0, 36:2	n/a	Terapontidae, <i>Terapon</i>	—	n/a
Melamphaidae	18:1	n/a	Terapontidae, <i>Leiopotherapon</i>	26:8	n/a
Menidae	4:2, 18:1, 23:1, 48:1, 49:0	n/a	Toxotidae	26:1, 42:1	n/a
Moronidae	27:1	n/a	Trachichthyidae	4:3, 39:1	n/a
Mugilidae, <i>Agonostomus</i>	9:0, 15:0, 43:0	n/a	Trachinidae	—	n/a
Mullidae	12:1, 32:2, 37:2	n/a	Triacanthodidae	9:2, 21:0, 29:1	n/a
Nandidae	9:0, 14:0	n/a	Tripterygiidae, <i>Lepidoblennius</i>	26:3, 34:1	n/a
Nematistiidae	43:1	n/a	Tripterygiidae, <i>Ruanoho</i>	—	n/a
Nemipteridae	16:1, 36:2, 40:1, 50:1	n/a	Uranoscopidae, <i>Xenocephalus</i>	11:1, 12:2, 37:1, 38:1, 45:0, 52:1	n/a
Ophidiidae, <i>Brotula</i>	16:1, 21:1, 40:1	n/a	Veliferidae, <i>Velifer</i>	4:3, 16:0, 17:1, 43:1, 48:1, 49:0	n/a
Ophidiidae, <i>Dicrolene</i>	7:0, 50:0	n/a	Zanclidae	7:1, 20:1	n/a
Opistognathidae, <i>Lonchopisthus</i>	38:1	n/a	Zaprionidae	23:1	n/a
Oreosomatidae	7:0, 11:1, 33:1	n/a	Zeniontidae	—	n/a
Ostracoberycidae	—	n/a			
Parazenidae	6:2, 10:2	n/a	1	14:0, 15:1	100
Pempheridae	—	n/a	2	30:1, 31:1	100
Percichthyidae	26:1	n/a	3	32:2	100
Percidae, <i>Perca</i>	31:0	n/a	4	14:1, 17:2, 18:1	100
Percidae, <i>Percina</i>	27:1, 30:1, 37:3	n/a	5	<u>9:3</u> , 26:5, 38:1, 50:1, 51:2	100
Percopsidae	16:0	n/a	6	45:1	99
Pholidichthyidae	<u>4:4</u> , 9:1, 32:0, 44:1	n/a	7	12:0, 13:1, 19:1	100
Platycephalidae, <i>Platycephalus</i>	20:1, 32:1	n/a	8	38:0, 50:0	99
Plesiopidae, <i>Assessor</i>	11:1, 42:1	n/a	9	9:2, 15:0, 21:1, 32:0	100
Polycentridae, <i>Afronandus</i>	—	n/a	10	6:2, 11:1, 39:1	100
Polycentridae, <i>Monocirrhus</i>	21:1	n/a	11	37:1, 41:1	100
Polycentridae, <i>Polycentropsis</i>	—	n/a	12	46:1, 48:1	100
Polycentridae, <i>Polycentrus</i>	45:0	n/a	13	35:0, 40:1, <u>55:1</u>	100
Polymixiidae	5:1, 45:0	n/a	14	3:1, 32:0	100
Polynemidae	17:1	n/a	15	30:0, 43:1	99
Pomacentridae, <i>Amphiprion</i>	45:0	n/a	16	11:1, 45:1	99
Pomacentridae, <i>Dischistodus</i>	—	n/a	17	6:2, 19:1, 44:1, <u>54:1</u>	100
Pomatomidae	12:1, 26:1	n/a	18	<u>2:1</u> , 40:0, 53:1, 55:0	100
Priacanthidae	18:1, 52:1	n/a	19	4:1, 10:2, 13:1	100
Pristolepidae	16:1, 31:0, 42:0	n/a	20	22:1	100
Psettodidae	17:2, 50:0	n/a	21	1:1, 37:2, 40:1	100
Pseudaphritidae	15:0, 17:1, 37:3	n/a	22	3:1	98
Pseudochromidae	7:1, 13:1, 37:1, 2	n/a	23	4:0, 35:1	98
Rachycentridae	4:1	n/a	24	32:0, 51:2	100
Ranicipitidae	3:1, 6:2, 12:2, 17:2, 37:1, 39:1	n/a	25	26:2, <u>28:1</u>	100
Rhamphocottidae	32:1	n/a	26	18:0, 27:1, 44:1, 50:1	100
Rhyacichthyidae	1:1, 12:2, 14:1, 29:1, 37:1, 44:1	n/a	27	32:3, 41:1	100
Rondeletiidae	—	n/a	28	—	100
Sciaenidae, <i>Cynoscion</i>	7:1, 12:2, 36:2, 45:1	n/a	29	9:0, 35:0	100
Scomberesocidae	1:0, 15:0, 40:0, 42:0	n/a	30	—	86
Scombridae, <i>Scomber</i>	4:3, 49:0	n/a	31	6:0	91
Scombrolabracidae	—	n/a	32	45:1	97
Scorpaenidae	—	n/a	33	16:1	97
Sebastidae	49:0	n/a	34	50:1	96
Serranidae	—	n/a	35	3:1, 11:1, 12:0	100
Sillaginidae	6:3, 21:1, 27:1, 47:1	n/a	36	52:1	98
Sparidae	—	n/a	37	27:1	97
Sphyracnidae	7:1	n/a	38	10:2, 20:1, <u>24:1</u> , 45:0	100
Stephanoberycidae	21:1, 39:1, 41:1, 44:1	n/a	39	22:1	100
Stichaeidae	—	n/a	40	4:2, 14:0	99
Symphysanodontidae	—	n/a	41	<u>10:1</u> , 45:0	100
Synbranchidae	37:2, 38:1, 42:1, 44:1, 50:0	n/a	42	1:1, 23:1	99

Table 13.—Continued.

Node	Supporting Characters	F	Node	Supporting Characters	F
43	26:6	98	92	11:1	100
44	40:1	97	93	15:1	100
45	4:0, 42:1	100	94	—	94
46	14:0	81	95	49:0	78
47	—	68	96	21:1	96
48	37:1	100	97	36:1	100
49	31:1	100	98	45:1	99
50	17:1, 43:1	100	99	26:6	100
51	20:1	100	100	49:1	100
52	17:2	97	101	7:1	100
53	—	75	102	12:1	93
54	50:1	90	103	17:1	94
55	21:1, 39:1	100	104	49:1	95
56	7:1, 18:1, 40:1, 43:1	100	105	9:1	100
57	16:1	100	106	18:1	100
58	1:1, 23:1, 32:1	100	107	6:1, 45:1	100
59	7:1	58	108	17:1	77
60	15:1, 18:1	100	109	21:1	92
61	12:2	83	110	12:2	96
62	—	81	111	49:0	88
63	7:0	81	112	26:7, 42:1	100
64	—	80	113	18:1, 52:1	100
65	37:3, 50:1	100	114	19:1	100
66	17:0	100	115	30:1, 31:1	100
67	30:1, 31:1	100	116	<u>36a:1</u> , 42:1	100
68	12:2	100	117	—	98
69	21:1	100	118	45:1	96
70	17:2	100	119	17:2	96
71	6:2, 37:1	100	120	5:1, 23:1	99
72	7:0, 39:1, 40:1, 44:1	100	121	—	89
73	11:1, 14:1, 36:1, 37:2, <u>38:2</u> , 41:1	100	122	11:1, 43:1	99
74	1:1, 35:1	100	123	21:0	98
75	9:1, 36:2, 43:1	100	124	—	99
76	11:0	100	125	25:1, 33:1	98
77	30:0, 31:0	100	126	50:1	100
78	—	91	127	—	96
79	—	89	128	—	91
80	43:0	92	129	26:6, 39:1	100
81	1:1, 53:1	91	130	12:2, 21:1	99
82	7:0, 14:1, 20:1, 39:1	100	131	43:0	96
83	15:1	100	132	17:0, 32:1	100
84	3:1, 11:1	100	133	50:1	100
85	—	98	134	14:1	100
86	4:3, 40:1, 52:1	100	135	38:1	100
87	32:2, 34:1, 39:1	100	136	26:6	99
88	—	97	137	7:1	100
89	—	99	138	52:1	100
90	52:1	100	139	11:0, 15:1, 43:1	100
91	6:3	100	140	4:3, 27:1	100
			141	10:2	99

chus and *Aulichthys* is polyphyletic, and that *Hypoptychus* and *Aulichthys* form a sister group, Hypoptychidae. In retrieving Ellassomatidae as sister group to a series of branches including Aulorhynchidae, Synbranchiformes, and Gasterosteidae, the arrangement in the MRT is congruent with Johnson and

Springer's (1997:176, abstract) first suggestion of a close relationship between Ellassomatidae and Gasterosteidae. The structure of the clade, and its retrieved sister group, are worthy of more study. Retrieval of Synbranchidae and Mastacembelidae as a monophyletic group and their inclusion as closely re-

lated to gasterosteiforms in Clade 2 variously supports the findings of J&P and other authors.

Clade [D 130]. Centriscidae (includes Macroramphosidae) have usually been treated as members of the Gasterosteiformes, among which they are considered most closely related to the Aulostomidae and Fistulariidae (Nelson 1994:302), which were not treated by S&J. Among other characters, centriscids, aulostomids, and fistulariids share in having the anterior vertebrae elongate. Chen et al. (2003) found molecular support for a close relationship of the three families.

We examined the gill-arch musculature and skeleton of two specimens of *Aulostomus chinensis* (Linnaeus), USNM 111979 (147 mm) and 327565 (221 mm) and find that it is very reduced and generally uninformative. Among other things, Eb4 is absent (also absent in *Fistularia*, J&P:table 1) and the posterior musculature is incompletely differentiated from SO. A small muscle, probably Ad5, attaches to the distal ends of Cb4 and Cb5; there is no indication of OP or ER, which does not occur in the absence of OP. A short, IAC (also present in *Fistularia*, J&P:table 1) attaches to Eb1 uncinat process, but does not join the well-developed Pb2, which lacks articulating processes. Nelson (1969a:fig. 17A) illustrated the gill-arch skeleton of *A. chinensis*.

S&J treated Centriscidae, Menidae, and Icosteidae as more probably related to pre-percomorph groups, because the three families possess ER and have OP attaching to or at the level of Cb4. Retrieval of the three families among a group of pre-perciforms by our MRT supports S&J's opinion. If the centriscids, aulostomids, and fistulariids are closely related, and their linkage with the other gasterosteiforms is corroborated, there are two main possibilities: the pre-perciform characters of centriscids are reversals (or new acquisitions), or centriscids represent the basal gasterosteiform branch, in which case, the gasterosteiforms are probably pre-perciforms.

ANABANTOMORPHA [A 13 to 17]. Britz (2003:427) proposed, but incompletely resolved the interrelationships of these fishes. The MRT retrieved the anabantomorphs as the basal series of steps leading to the Percesoces, hence the anabantomorphs are indicated as polyphyletic without inclusion of Percesoces. Character 55 (parasphenoid teeth) was inadequate to define the anabantomorphs, but character 54 (Eb1s modified as suprabranchial organs) did define the Anabantoidei [A 17]. We believe the anabantomorphs (and anabantoids) are monophyletic, and that the intrarelations of the families in our analysis are probably ((Nandidae + Badidae) + (Pristolepididae (Channidae + Anabantidae))). We have no suggestion as to their nearest relatives, but do not exclude the Percesoces as a possibility.

Apparently, ours is the first cladistic analysis to

indicate a close relationship between anabantomorphs and Percesoces. Without suggesting a direct relationship, Gosline (1968), in a survey of perciform fishes, uniquely segregated these two groups (as Anabantoidei, Mugiloidei) as the only "Protopercoid" Suborders (our emphasis) of his "Percoidei and Derivative Suborders." In part following Regan (1912), Gosline's Mugiloidei included the Polynemidae, Mugilidae, Sphyraenidae, Atherinidae and Phallostethidae, but excluded the "cyprinodontoids" (= our Cyprinodontiformes) and "exocoetoids" (= our Belontiiformes), which he placed among the perciforms, and his Anabantoidei excluded *Pristolepis* and *Nandus*, which he also placed among the perciforms.

Gosline's main character for associating his Mugiloidei and Anabantoidei, was a plesiomorphic condition, separation of pelvices from cleithra. He recognized that there were problems with the character and that reversals to the plesiomorphic state had probably occurred. Although Gosline did not resolve the classification so neatly as does our MRT, we believe there was more than luck involved in his perception.

LABROIDEI, PHOLIDICHTHYIDAE [A 5]. The MRT implies that the Labroidei are paraphyletic without inclusion of Pholidichthyidae, thus essentially corroborating Stiassny and Jensen (1987), who most recently hypothesized a monophyletic Labroidei (Embiotocidae, Pomacentridae, Cichlidae, Labroidea) based on gill-arch morphology. They lacked material of *Pholidichthys*, but noted (their p. 294) several osteological similarities shared by that genus and labroids, and indicated that a study of *Pholidichthys* musculature would be important, particularly as to whether it included a "sling" (a joining of LE4 and OP). It does not—it lacks LE4, but even if S&J are incorrect in identifying the single levator on Eb4 as LP, rather than LE4, there is no muscular continuation of the levator with OP.

Johnson (1993:8–10) noted problems with some of Stiassny and Jensen's characters and hoped that "the hypothesis of a monophyletic Labroidei does not become dogma" in the "absence of corroborative evidence independent of the pharyngeal apparatus." He believed that "labroid monophyly will be an important hypothesis to test with molecular data."

Using single-copy nuclear DNA, Streelman and Karl (1997), who lacked material of *Pholidichthys*, tested the monophyly of Stiassny and Jensen's Labroidei. They used *Sebastes* (Sebastidae) as outgroup in their analysis and included a cottid, percoid, pomacanthid, and acanthurid together with three or more taxa in each of the labroid families. Their results (their fig. 2) indicate a polyphyletic Labroidei: ((Embiotocidae + Pomacentridae) + (Cottidae (Percidae (Pomacanthidae (Acanthuridae (Labridae + Cichlidae)))))

Given that the monophyly of the Labroidei, including *Pholidichthys*, still rests only on morphology of gill-arch muscles and skeleton, our addition of more characters from the same anatomical complex may only be adding correlated characters. Polyphyly of the group has been hypothesized by only one molecular study, which included relatively few non-labroids and did not include *Pholidichthys*. Molecular studies involving labroids, *Pholidichthys*, and non-labroids additional to those used by Streelman and Karl (1997) are still needed, as are morphological studies based on more than gill-arch anatomy.

POLYCENTRIDAE [C 60]. Both the MRT and SCT recovered Polycentridae and Batrachoididae as a monophyletic clade. As discussed under Batrachoidiformes, we doubt a close relationship between the two groups. S&J provide several non-gill arch specializations in support of polycentrid monophyly, which we believe will continue to be corroborated by future studies.

NOTOTHENOIDEI (BOVICHTIDAE, PSEUDAPHRITIDAE) [C 69 and B 34]. The MRT retrieved the essentially southern hemispheric restricted notothenioids as polyphyletic. Pseudaphritidae were retrieved as a branch of a polytomy including an apparently heterogeneous assemblage of perciform and pre-percomorph taxa. Bovichtidae were retrieved as the sister group of the zoarcoid family Stichaeidae. The sister group is the fifth step in a multi-stepwise clade [C 64] whose first four steps are Plesiopidae (perciform), Bathymasteridae (zoarcoid), Zaproridae (zoarcoid), Anoplopomatidae (traditionally allied with scorpaenoids, but Quast, 1965, questioned the relationship, and the matter has not been resolved).

The monophyly of the notothenioids has long been accepted (Balushkin 1992:90–91, references the main publications). Balushkin (1992, 2000), based on morphology, hypothesized the Pseudaphritidae and Bovichtidae as the first and second branches of the notothenioid clade. Near et al. (2004), using complete gene sequences of mtDNA and 16S rRNA, found Bovichtidae and Pseudaphritidae as the first and second branches.

The position of Bovichtidae as closely related to zoarcoids appears to offer the first cladistic support for this relationship, which has been generally suggested (Anderson 1984:581, 2003:309; Nelson 1994:388). Molecular studies (Chen et al. 2003), however, have not found a close relationship between the two groups.

DACTYLOPTERIDAE, CALLIONYMOIDEI, GOBIESOCOIDEI, BLENNOIDEI. The MRT retrieved this group as a completely resolved monophyletic clade [C 71]. Some of the implied relationships are new, but we believe that the group is worth serious consideration. For this reason we assign a new ordinal-group name, **Benthomorpha**, to it. Perhaps, the most questionable

member is the Dactylopteridae, which Imamura (2000) hypothesized as including Malacanthidae. Our MRT retrieved the latter family as part of a polychotomous clade [D—see polytomy] well removed from the Benthomorpha. One of the main characters, a ring-like TPb2, that Imamura used to relate the two families is present in a wide variety of acanthomorphs (e.g., Chaunacidae, Percidae, Kuhliidae, Bathymasteridae). We did not use this character state in our analysis because the many different shapes with intermediates that TPb2 assumes makes it difficult to code.

Callionymoidei are universally recognized as monophyletic and comprise the Draconettidae and highly specialized Callionymidae, which we did not include in our analysis. The callionymoids are generally considered to be closely related to the Gobiesocoei (Gosline, 1970; Allen, 1984:629; Nelson, 1994:409; Leis and Carson-Ewart, 2000:131). Nelson (1994:409–410) summarized the literature, citing dissenting authors, and mentioned that there was no osteological study that demonstrated a cladistic relationship between the two groups. Springer (1993) hypothesized the monophyly of the Blennioidei [C 74] and removed it from close relationship to the “Stichaeoidei” (= Zoarcoidei of current authors). Johnson (1993:10) and Mooi and Gill (1995:130) reported additional synapomorphies for the Blennioidei, and its monophyly is currently strongly entrenched. A morphologically based close relationship between the Gobiesocoei and Blennioidei has not been hypothesized, although Rosen and Patterson (1990) noted considerable similarity in the dorsal gill-arch skeleton of both groups. Chen et al.’s (2003:fig. 5) molecular-based study, however, retrieved a monophyletic clade ((Blenniidae + Tripterygiidae) + (Gobiesocidae)) in their simultaneous analysis; the first two families represented by one taxon each, and the third by two taxa. Support for all of Clade [C 71], except possibly for inclusion of Dactylopteridae, appears to be accumulating.

In spite of many years study of blennioids, Springer has not suggested a sister group for them. Springer (1993) did, however hypothesize the monophyly of each of the blennioid families except the Labrisomidae, proposing the Tripterygiidae as sister group of all other blennioids. Springer also did not hypothesize the interrelationships of the other families. Although not resolving a monophyletic Tripterygiidae, Clade [C 73] does accord with Springer’s proposed position of the family (which is monophyletic based on other characters). No one has hypothesized a monophyletic Labrisomidae, and Springer (1993:493) suggested that there was possibly a continuum of taxa joining Labrisomidae and Chaenopsidae, including *Neoclinus*, which he “arbitrarily” included in the Labrisomidae. Stepien et al. (1993), using

rDNA and allozyme data and Tripterygiidae and Blenniidae as outgroups, analyzed the interrelationships of three families of blennioids, Clinidae [Myxodinae], Labrisomidae, Chaenopsidae. Their most parsimonious results suggested (Chaenopsidae + (Labrisomidae + Chaenopsidae)), but the allozyme data suggested that Labrisomidae are paraphyletic. In a morphological study using an array of blennioid taxa as outgroups, Hastings and Springer (1994) hypothesized a monophyletic Chaenopsidae in which *Neoclinus* was retrieved as the sister-group of all other chaenopsids. They did not hypothesize a sister group for their Chaenopsidae, and left open the possibility that its composition might change in a more comprehensive analysis. Considering the trend, it appears reasonable to synonymize Labrisomidae Hubbs (1952:56) with Chaenopsidae Gill (1865:141).

SPAROIDEI, CALLANTHIDAE [D 114]. Johnson (1980:20), based on anatomy, first proposed Sparoidei to comprise Sparidae, Centranchidae, Lethrinidae, Nemipteridae. Carpenter and Johnson (2002), in a morphological phylogenetic study, corroborated this composition. Orrell et al. (2002), in a molecular study, found support for monophyly in only one of their two analyses: weighted cytochrome *b* nucleotide analysis. Their equally weighted nucleotide analysis, has ((Nemipteridae + Lateolabracidae + Moronidae) + (other sparoids)). Orrell and Carpenter (2004), in another molecular study, using 16S rRNA and cytochrome *b* retrieved only a polyphyletic Sparoidei. Neither of the molecular studies included Callanthidae among its outgroups, but almost all the families used in the outgroups were included in our analysis.

SILLAGINIDAE (PERCIDAE + RHYACICHTHYIDAE) [C 49]. These three families were retrieved as a monophyletic clade in a polytomy [C] with a variety of other fishes. In spite of considerable effort on the part of many workers, the interrelationships of the Gobioidae have not been convincingly hypothesized. Winterbottom (1993b), made the most complete morphological search for a gobioid sister group. He described 23 putative gobioid apomorphies and found that the scorpaenoid Hoplichthyidae, among all the families he studied, exhibited the greatest number, 11, of these apomorphies, but he was unsatisfied that a close relationship existed between the two groups. Miya et al. (2003:fig. 2) retrieved the gobioids as the sister group of the Dactylopteridae, which, as noted above, we retrieved as sister group to a callionymoid, gobiesocoid, blennioid clade [C 72].

Perhaps of interest, is the appearance of Sillaginidae as a close relative of Percidae. McKay (1985:1–2) discussed the classificatory history of the sillaginids and quoted “W. Schwarzhans *pers. comm.*” as having informed him that based on otoliths, “I have little doubt that [the percid] *Aspro* (= *Zingel*) really is the closest relative to the sillaginids.” McKay went

on to write, “It appears that the family Sillaginidae is related to the Sciaenidae, Percidae, and to a lesser extent the Haemulidae.” Although our analysis did not retrieve haemulids or sciaenids in a clade near sillaginids, we believe that sillaginids are probably most closely related to sciaenids. If *Zingel* is not sister-group of all other percids, any similarity to the sillaginids is undoubtedly convergent.

MISCELLANEOUS FAMILIES. Menidae [D 130] were discussed, in part, under Smegmamorpha. Although S&J’s suggestion that Menidae are a pre-perciform family is supported by the MRT, Chen et al. (2003) found Menidae to be enmeshed in a perciform clade of carangoids in two of their three analyses and in their simultaneous analysis. In the third analysis (their fig. 3), Menidae is in a clade with a sphyraenid, a polynemid, and a bothid, and this clade is sister to a clade with more pleuronectiforms, a latid, and several carangoids.

SPHYRAENIDAE, POLYNEMIDAE [D 124]. These two families were retrieved by our MRT as a sister group. Sphyraenidae and Polynemidae were originally associated closely by Regan (1912:846–847; fully quoted in Gosline, 1962:210, who essentially agreed with Regan’s assessment). Johnson (1993:7–8) discussed the problematic classificatory history of the two families beginning with Gosline (1968), and concluded that the evidence favored a Polynemidae-Sciaenidae sister group. Johnson (1986:fig. 1) hypothesized that the Sphyraenidae are part of a scombroid clade: (Scombridae (Pomatomidae (Sphyraenidae (Scombridae))). In our MRT, the Sphyraenidae-Polynemidae clade is only one step removed from Scombridae in the clade [D 123] comprising these three families, but which includes no other scombroids. Orrell et al. (2003), in a molecular study, found no support for inclusion of Sphyraenidae in the Scombroidei. The resolution of sphyraenid and polynemid interrelationships remains problematic.

ICOSTEIDAE [D 132] were discussed, in part, under SMEGMAMORPHA. S&J presented both gill arch and non-gill arch evidence that the family is probably most closely related to stephanoberyciforms. The MRT retrieved the Icosteidae as sister group of a pair of clades, one [D 134], comprising four of the five stephanoberyciform families included in our study, and the other [D 137], comprising a mix of Holocentridae, Ranicipitidae, and Ophidiiforms, thus lending support to S&J’s conclusion.

CARANGOIDEI. Our analysis included four of the five carangoid families: Nematistiidae, Coryphaenidae, Rachycentridae, Carangidae (Echeneidae, not included). These were retrieved in three well separated clades [D 97, 98, 110]. Only Rachycentridae and Carangidae appear as closely related.

HAEMULIDAE, INERMIDAE. These two families were

retrieved as a sister group [D 113], thus corroborating Johnson's (1980:46–48) hypothesis.

GIRELLOIDEI. Johnson and Fritzsche (1989:15) concurred with Freyhof's (1963) hypothesis that the Ramus Lateralis Accessorius nerve pattern 10 characterized a natural assemblage of fishes. They considered RLA pattern 10 as the synapomorphy uniting Girellidae, Scorpididae, Kyphosidae, Microcanthidae, Kuhliidae, Arripidae, Oplegnathidae, Terapontidae, and Stromateoidei, but did not provide a name for the group. S&J excluded the stromateoids and applied the ordinal-group name Girelloidei to the remaining families. Of the Girelloidei, only Girellidae, Kuhliidae, and Terapontidae are included in our analysis, but we include the stromateoid Centrolophidae and its putative relative, Amarsipidae, here for purposes of discussion. The MRT retrieved each of these families either in well separated clades or well separated within a highly branched clade, and the well-defined Terapontidae (Vari, 1978) was retrieved in two separate clades. The results probably indicate that gill-arch muscle and skeletal morphology as considered here are either not useful in defining girelloid intra-relationships or that the Girelloidei are polyphyletic.

GRAMMATIDAE, OPISTOGNATHIDAE, GERREIDAE, PSEUDOCROMIDAE. These four families form the four basal stepwise clades of a series of clades [A 4] terminating in (Labroidei) + (Anabantoidei, Percosces). The Pseudochromidae and Opistognathidae have long been associated, but usually together with other currently recognized families. Jordan and Snyder (1902:492) appear to be the first to have proposed that the two are "very closely related."

Mok et al. (1990:38) first hypothesized a monophyly clade of three of the families, indicating (Pseudochromidae (Grammatidae + Opistognathidae)). Mooi and Gill (1995:121), however, disputed one of Mok et al.'s characters, nature of the M. epaxialis association with the dorsal-fin pterygiophores, and further commented, "Our continuing studies on the phylogenetic positions of Grammatidae, Opistognathidae and other pseudochromoid families have failed to provide corroborating evidence for a sister-group relationship between the Grammatidae and Opistognathidae." This statement does not appear to reject the possibility that Mok et al.'s three families are closely related.

Mok et al. (1990:38) hypothesized that the Plesiopidae (including the Acanthoclinidae) are the sister group of the pseudochromoid families. Our analysis has the Plesiopidae in a clade [C 64] well removed from the Pseudochromidae.

In conclusion, a morphological cladistic analysis based on a single complex character set strongly corroborates some previously hypothesized phylogenies based on different characters, partially supports others, has no bearing on yet others, suggests possible relationships that are worth further research, and implies relationships in some cases that seemingly make no sense. The confusion is partly due to the taxa we chose to include and the incomplete spectrum of taxa that we had available to include, as well as to the restricted character complex. Although taxon-rich character-poor phylogenetic analyses currently can involve extended computer time and result in considerable homoplasy, we believe even more expanded studies than ours will contribute to refinement of the ore from Rosenblatt's mining operation.

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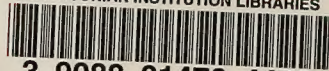
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